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WINTER SOIL TEMPERATURES AND THEIR RELATION TO SUBTERRANEAN INSECT SURVIVAL[1]

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INTRODUCTION

The studies on winter soil temperatures discussed in this paper are a development of work done at the University of Minnesota on wireworms (Elateridae) during the winter of 1927–28. The data obtained are, however, of wide application, affecting as they do every form of insect life which is passed in the soil in any stage, be it egg, larva, pupa, or adult. Not only entomologists but also agronomists and engineers are interested in heat conduction through soil, though the interests of the latter are in depths much below those studied here. Nevertheless, a similar technic to that here described could readily be used in following temperature waves downward to any required depth.

It has, of course, long been known that a snow blanket insulates the soil against subzero air temperatures. But, numerous as have been the workers on soil temperatures, there can be found but few instances where exact measurements have been made of the degree of protection which snow affords.

Sweezey (*18*),[3] Bouyoucos (*1*, *2*), and McColloch and Hayes (*9*) have, among others, made extensive soil-temperature studies, but from different angles and with varied technic. The work of Sweezey is valuable because it represents the records of a long term of years and at a variety of depths. Bouyoucos studied the influence of the various intrinsic factors affecting soil temperature to a depth of 18 inches under controlled and natural conditions, and the relationship between the soil temperature and the different meteorological elements. McColloch and Hayes, like the writer, were interested in soil temperature from the standpoint of the insect survival, but their technic was altogether different from that herein described. They were interested primarily in the effect of soil temperatures on the migration of white grubs in the larval and adult stages, whereas this paper deals with the effect of subzero temperatures on insects which normally overwinter in the upper 2 feet of soil.

The records here presented cover a period of eight months, from October 1 to June 6, by which date spring conditions had been established.

[1] Received for publication Apr. 15, 1930; issued October, 1930. Published with the approval of the director as paper No. 906 of the Journal series of the Minnesota Agricultural Experiment Station. The bulk of the work on which this paper is based was done in the laboratories of the division of entomology, University of Minnesota, and a small portion at the Montana Agricultural Experiment Station.

[2] The writer gratefully acknowledges his indebtedness to Dr. William Robinson, Dr. R. N. Chapman, Prof. A. G. Ruggles, Dr. F. G. Holdaway, and H. E. Gray for helpful criticisms and assistance.

[3] Reference is made by number (italic) to Literature Cited, p. 591.

METHODS AND APPARATUS

The thermocouple method of taking soil temperatures was used in preference to that of soil thermometers because of its simplicity and accuracy. Connell (*4*) describes an efficient method of taking soil temperatures, using an iron pipe and standard thermometer, but for winter work this method would be much less convenient. Sweetman used the thermocouple method at Minnesota for two years with good results, and the apparatus herein described is a modification of his set-up. Robinson (*15*) has described the principle of the thermocouple so very clearly that any discussion here is needless.

It was desired to obtain soil temperatures at intervals of 2 inches (5.08 cm.) from soil surface to a depth of 2 feet (60.96 cm.), in two different situations, one where the ground was allowed to retain its normal covering of snow and the other under bare earth. The buried part of the apparatus consisted of two pieces of 1 by 12 inch board 3 feet long, to which all the junctions were affixed. The object of attaching them to a solid base was to facilitate the sinking of the junctions to the required depth and to insure that they would maintain their relative positions. Each board was, in this particular instance, prepared by boring holes three-sixteenths of an inch in diameter, these holes being staggered on each side of a center line and with a 4-inch vertical distance between the holes. A constantan wire of 28 gage was led down the center of the board to the 24-inch hole where a junction was made with a copper wire of the same gage. The constantan wire was tapped by short leads to the remaining holes and at each hole a junction was made with a copper wire. The reason for having the junctions separated by a horizontal distance of about a foot was to insure that the temperature set up by one junction would not affect the reading of the next junction only 2 inches distant. The 12 copper wires had been previously shellacked and twisted into 40-foot cables and these inclosed in two lengths of ⅛-inch rubber tubing as insulation. (These cables can, of course, be of any desired length within reasonable limits, depending on the distance of the buried junctions from the recording instruments.) The copper-constantan junctions were then pushed through the holes in the board until they projected about 1½ inches. A 3/16-inch shell vial slipped over each junction and fitted tightly into the hole. No wires were left exposed, all short leads being insulated in rubber tubing. Absorbent cotton soaked in shellac was plugged on each side of any break in the rubber insulation to prevent air circulation and to make the system as nearly waterproof as possible. All breaks in the rubber tubing were wound with rubber and friction tape to render the joints waterproof. The network of insulated wires was then fastened securely to the board with clamps. (Figs. 1 and 2.)

Holes of the required depth were dug and the boards placed therein in a vertical position. The earth removed was well puddled with water and poured slowly into the holes so that the junctions would be thoroughly embedded. After the excess water was drained off, the resulting depressions were filled to the level of the ground surface and the system left for some weeks to come to equilibrium with the surrounding soil before readings were taken.

The constantan wires from each board were soldered together and a single constantan lead was run to the switchboard.

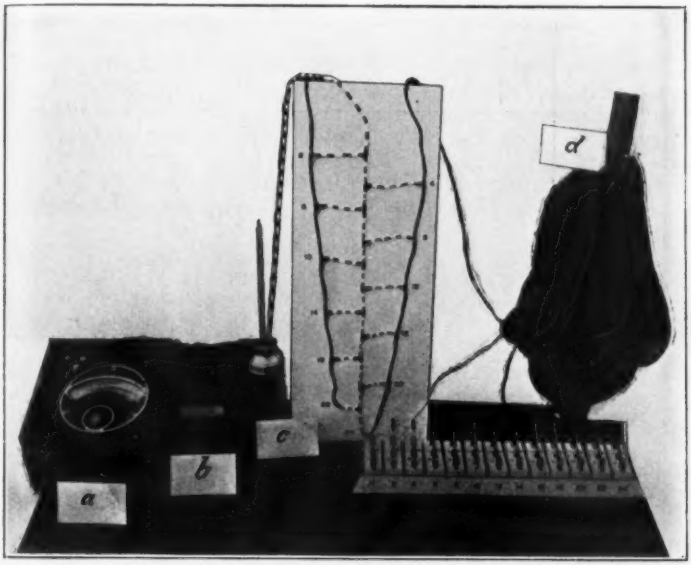

FIGURE 1.—Apparatus used for measuring soil temperatures: *a*, Pyrovolter; *b*, outside galvanometer; *c*, thermos bottle with junction at known temperature; *d*, 40 feet of wire cable connecting inside switchboard with buried junctions

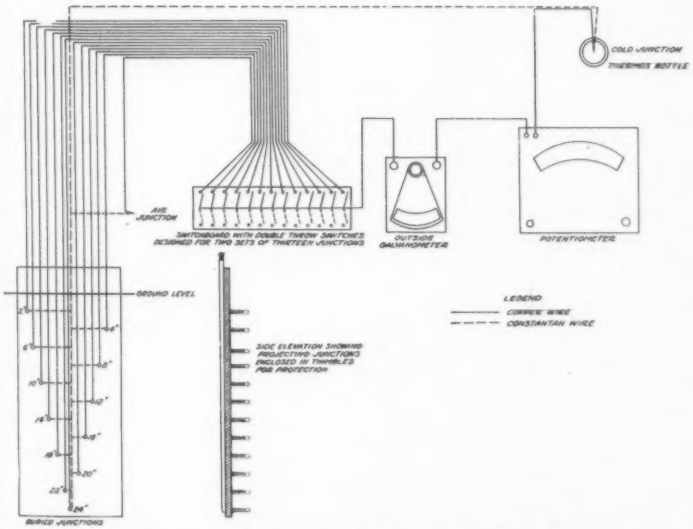

FIGURE 2.—Diagram of system of wiring used in soil-temperature apparatus

The rest of the apparatus was erected on a table inside a heated building adjacent, so that readings could be taken at any time and under any weather conditions. The 12 leads from the snow-covered junctions were connected to the poles of a battery of single-pole double throw switches. The leads from the bare-earth junctions were connected to the other terminals. The constantan wire was led to the cold junction which was in a thermos bottle containing cracked ice and water at 0° C. registering the known temperature. The copper wire from this "known" junction was connected through a pyrovolter and outside galvanometer to the common terminals of the switchboard.

The throwing in of a switch gave the reading at a single depth and in either of the two situations, depending on which way the switch was thrown. An additional junction for air temperature was also added to the system, this being fastened to the side of a post outside and in the shade.

Temperatures were taken every two days during most of the period of the study, and at about 8 o'clock in the morning. As the days lengthened in the spring, readings were taken at an earlier hour.

The mean air temperature was plotted from the records of the United States Weather Bureau, Minneapolis station.

SOIL-TEMPERATURE DATA

There are two sources of heat by which soil temperature may be affected (1) the radiant energy from the sun, and (2) internal heat conducted to the surface from below. The internal heat of the earth, in which the temperature rises 1° F. for every 100 feet of penetration into the earth, is negligible in these experiments, as only the first 2 feet of soil are being studied.

In temperate regions, daily variations of temperature cease to be felt at depths ranging from 2 to 3 feet, according to the nature and condition of the soil. Monthly variations are felt to much greater depths, and in the Temperate Zone, e. g., Paris and Brussels, annual variations do not disappear at a depth less than 75 feet (*7, p. 302–303*). Smith (*17, p. 80*) puts the limit of annual variation at 40 feet in depth, but in any case it is too deep to be of any significance in a study involving merely the surface layers. The solar heat descends in waves, the effect of which can be followed for some days at the lower depths. The effect of a few warm days before a sudden cold spell is still in evidence after some days of reduced temperature. This lag is clearly demonstrated in Figure 3, where two days of warm weather between October 9 and 11 caused a corresponding rise immediately at the 2-inch level but did not affect the 8-inch level until October 13, and the 16-inch level until October 16. The effect of sudden rapid variations in temperature is not felt at depths much beyond 1 foot, only spells of warmth or coolness lasting for more than a day being able to affect the greater depths. The temperature of the upper layers follows closely the atmospheric changes, but the farther one penetrates the smoother is the curve obtained, and at 2 feet daily fluctuations are very small. The weekly variations at 2 feet are, of course, greater, and the seasonal variation is still more pronounced at that depth. Thus we find, in the fall and spring of the year, when hot days and cool nights are the rule, that the shallower depths follow,

with a decreasing correspondence, the fluctuations of the air temperature, while the lower depths show rather a correspondence with the

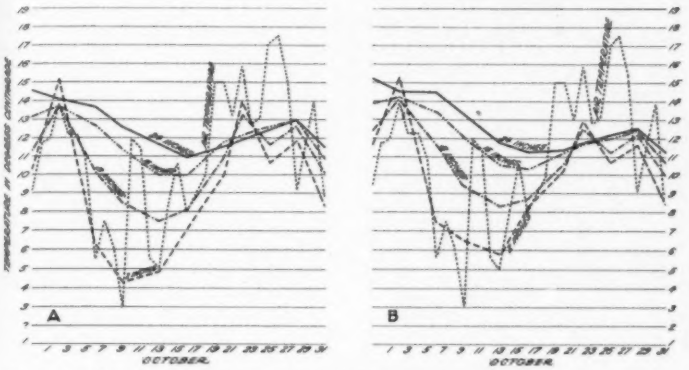

FIGURE 3.—Air temperatures and soil temperatures at different depths in bare (A) and sod-covered (B) ground during October

means of increasingly longer intervals. (Figs. 3, 4, 5, 6.) Under these conditions the charted lines for the shallower depths will cut

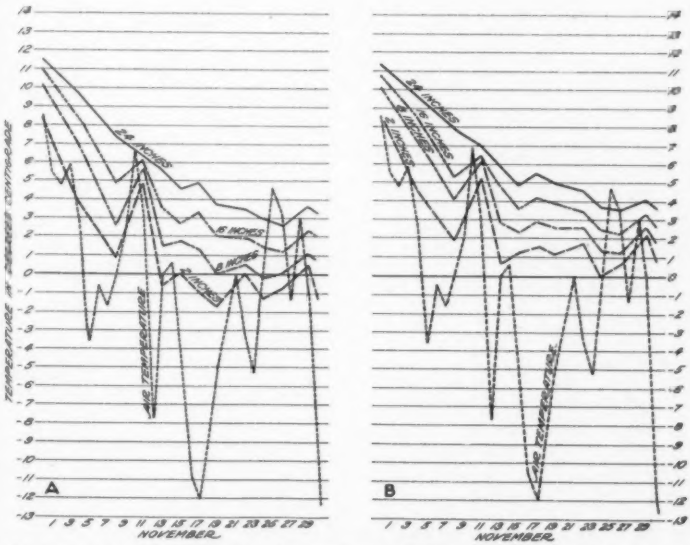

FIGURE 4.—Air temperatures and soil temperatures at different depths in bare (A) and sod-covered (B) ground during November

those of the depths more remote from the surface in several places; as witness the situations figured on October 1 and 22 (fig. 3), January

13 (fig. 7), February 7 (fig. 8), and April 16 (fig. 5), to quote only a few instances. At these points, contrary to the expectation in winter

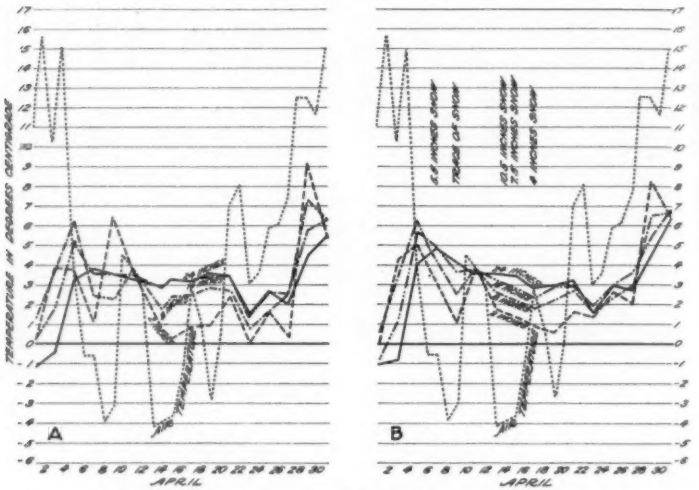

FIGURE 5.—Air temperatures and soil temperatures at different depths in bare (A) and snow-covered (B) ground during April

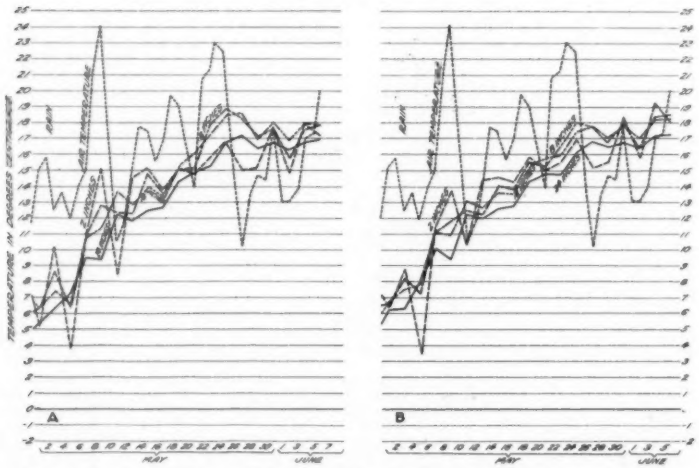

FIGURE 6.—Air temperatures and soil temperatures at different depths in bare (A) and sod-covered (B) ground during May and early June

temperatures, the 24-inch level is coldest, the 16-inch level slightly warmer and so on until the 2-inch level is reached, which shows the highest temperature.

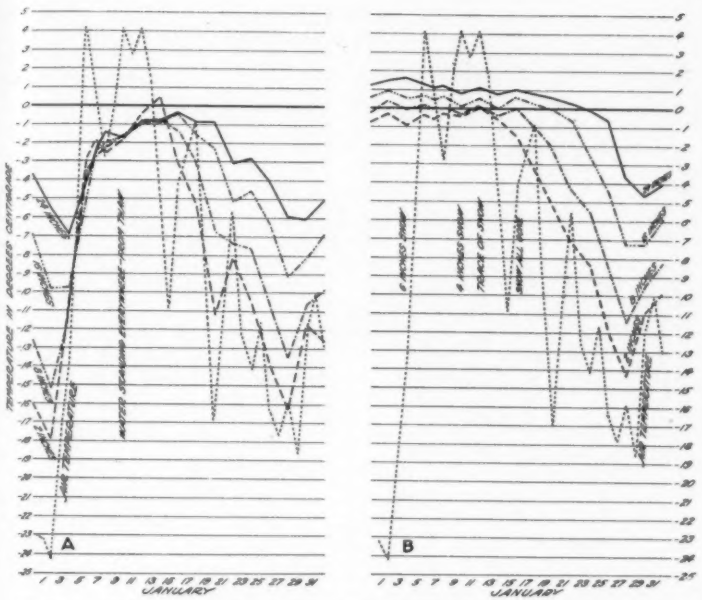

FIGURE 7.—Air temperatures and soil temperatures at different depths in bare (A) and snow-covered (B) ground in January

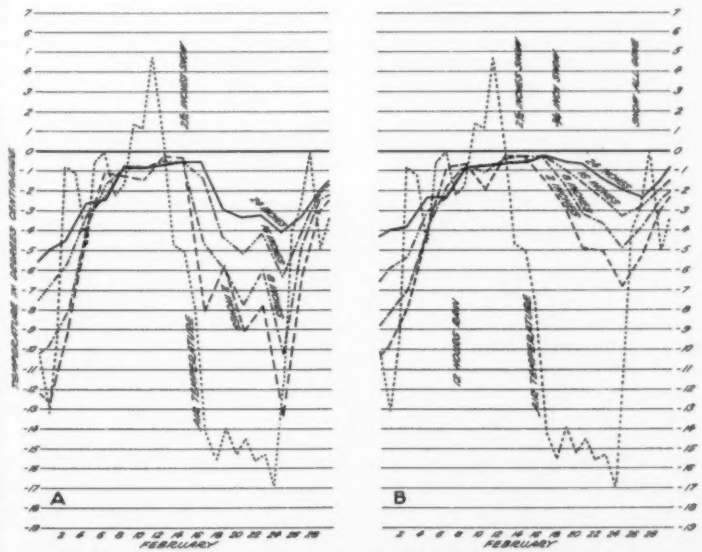

FIGURE 8.—Air temperatures and soil temperatures at different depths in bare (A) and sod-covered (B) ground in February

FALL AND SPRING INVERSION

We find, in lakes, a temperature stratification with the warm and disturbed epilimnion above, the stable and cool hypolimnion below, and the shifting but definite thermocline between them. In the spring and fall the waters of the whole lake are of about uniform density and we observe the phenomenon of a complete cirulation of all the water. Similarly in the soil, while the absence of circulation inhabits a true turnover in the sense in which it is found in lakes, yet there is a temperature movement which is to some extent comparable. At these times a complete reversal of temperature conditions is observed. In warm countries there are two times in the day when the direction of heat movement is changing. During the day heat is moving downward in the upper layer of the soil and during the night it is moving upward. The point where there is momentarily no movement is called by McKenzie and Williams (*12*) the thermostatic point. In this study, because of the time between observations, these thermostatic points are only in evidence in the fall and spring, their positions being indicated by the crosssing of the temperature curves for the different levels. During the hot summer months the surface layers of the soil are much warmer than are the lower layers. During the cold months the soil at greater depths is warmer. This inversion commonly takes place in the fall and spring in temperate regions, though unusually warm spells in the winter will cause partial inversions. A complete inversion, however, only occurs when the mean air temperature is above the freezing point. Fully as great fluctuations of the mean air temperature as is shown on the dates mentioned above, occur in November (fig. 4) and during practically the whole month of December (fig. 9), but if these fluctuations occur when the mean air temperature is less than 0° C., the inversions do not take place. In several instances where a series of fluctuations culminated in a rise of the mean air temperature to almost 0° an inversion almost occurred, there being less than a degree of difference in spread between the 2-inch and 24-inch levels, and on February 6 (fig. 8) the inversion occurred when the mean air temperature reached 0°, but here the spread between the top and bottom levels was less than 1.5°.

In the spring of the year the air means fluctuate rapidly and sharply and the succeeding warm and cold waves through the soil result in a chaotic crisscrossing of the temperature lines during this period with, however, a relatively small spread. During the winter months, on the other hand, fluctuations of equal rapidity and spread do not so markedly affect the internal soil temperatures, and a greater spread is maintained between the temperatures of the upper and lower levels. In general, it would appear that variations of the air temperature which occur above 0° C. affect the internal soil temperatures to a much greater degree than do similar fluctuations below the zero line, i. e., in the absence of snow or other insulation. The reason, of course, why subzero temperature changes do not so markedy affect the internal soil temperature is that in winter the ice in the soil has first to be melted, the heat of fusion being 80.02 gm. calories. Water possessing such a high heat capacity, five times greater than that of dry soils, requires five times as much heat to raise the temperature of a unit of water to 1° as is necessary for a unit weight of soil.

As the specific heat of water is so much higher than that of any soil it therefore follows that masses of water act powerfully in the moderation of soil temperature by their mere presence. The immediate effect of a warm wave is not evident in ice-filled soils and a lag results. A rise in air temperature from −23° to −6° C., that is 17°, through five days, resulted in a corresponding rise in the 24-inch level of only 0.75° five days after the commencement of the upward movement. But an almost corresponding situation in the above-zero part of the scale, that is a rise of the mean air temperature from −3° to +15°, or 18° in five days, resulted in a rise of the temperature of the 24-inch level of 5°, five days after the commencement of the upward movement. Here is a comparable rise in air temperature above and below the zero line, but the effect on the deeper soil temperatures compared to those of the upper strata is markedly different.

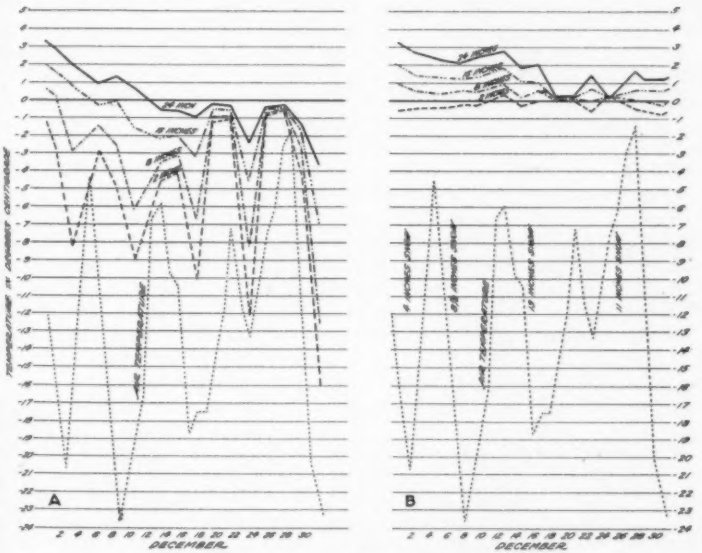

FIGURE 9.—Air temperatures and soil temperatures at different depths in bare (A) and snow-covered (B) ground in December

McKenzie-Taylor and Williams (*12*) show in their study of sand temperatures that the reduction in temperature range was approximately constant for a constant increase in depth. Given a known surface temperature they were able to calculate mathematically the temperature at any depth, and the observed and calculated temperatures were in remarkably close agrement. With soil, however, this agreement between the calculated and observed range was absent. Soil, unlike sand, is so lacking in uniformity of composition, and so many factors enter into the question of its heat conduction that ordinarily it is almost impossible to compute mathematically the temperature at a given depth from a known surface temperature.

Extremes of temperature, i. e., maxima and minima, especially during the winter months are more significant than monthly or even

weekly means in so far as the ability of an insect to hibernate is concerned.

EFFECT OF SNOW ON TEMPERATURE OF THE SOIL

The temperature records obtained from a situation where there is a surface insulation of snow differ, as one would anticipate, very markedly from those from bare ground subjected to the same air-temperature conditions. Bouyoucos (*2*) studied the effect of snow on the soil temperature for several winters, and for one month of his studies made comparisons of soil temperatures under the following conditions: (1) Bare, (2) covered with compacted snow, (3) covered with uncompacted snow, and (4) covered with a layer of vegetation and uncompacted snow. His findings are very similar to those shown here. A comparison of Figures 3 and 4 shows that for the months of October and November the temperatures in both the bare and sod-covered ground paralleled each other very closely, the slight lag in the temperature lines of the latter being due to the insulating effect of the sod covering. On December 1, 3½ inches of snow fell, and during the period from the first to the fifteenth there accumulated 15 inches of snow, which did not wholly disappear until January 12. From November 30 until January 5 the mean air temperature was never above 0° C., and for several days was below −18°, reaching a minimum of −24.2° on January 2. The temperatures recorded for the bare ground during this period closely followed the sharp fluctuations of the air temperature, the lowest temperatures recorded from the different levels being: Air, −24.2 ° C.; 2-inch level, −17.94°; 8-inch, −15.24°; 16-inch, −9.78°; 24-inch, −5.46°. These temperatures show, for January 2, a spread between the 2-inch and 24-inch levels of 12.48 °.

During this same period, under a snow blanket of varying thickness, the soil temperature in no case fell below −1.0° C., the greatest spread between the 2-inch and 24-inch levels being only 3.5°, and at one time it was only 0.4°. By January 13 the snow had all disappeared and the temperature in both situations became more nearly similar, except for the slight lag due to the insulating effect of the sod. Even a slight fall of 0.5 of an inch of snow on January 30 was sufficient to effect a rise in the temperature of the 2-inch level, whereas the accompanying 3° drop in air temperature on that date was followed by a corresponding drop in the temperature of the 2-inch level under bare ground. Snow, therefore, even an inch or two, makes a remarkable difference in soil temperatures and, of course, in the chance of survival of the soil-inhabitating organisms, and may quite conceivably be a limiting factor in their ability to overwinter successfully.

EFFECT OF RAIN ON TEMPERATURE OF THE SOIL

Several hours' rain, even in frozen soil, had the effect of bringing the soil temperatures to equilibrium in the layers studied. That is to say, the temperature spread between the 2-inch and 24-inch layers was narrowed, in one case to 0.4° C. and in another to 0.3°. Cessation of the rain and the subsequent drying out of the soil resulted in a widening of the temperature gradient at the different depths.

Normally the soil moisture consists of hygroscopic and capillary water, the amount of the latter depending largely on the physical nature of the soil and its relation to the underlying water table. Since this is the case, the majority of the temperatures here discussed, being those of similar soil in practically the same locality, and with merely a surface-covering difference, can be compared directly as an indication of soil conductivity, the water being a constant factor. When, however, a rain of some hours' duration occurs there is introduced "free water," which, as it penetrates into the soil, mechanically destroys the temperature gradient which is one criterion of soil conductivity, and the soil temperatures then obtained are those of the free water modified by the specific heat of the soil and other intrinsic factors.

On February 7, 1 inch of rain fell during a 12-hour period, followed by a marked rise in air temperature. (Fig. 8.) The soil-temperature gradient in both situations studied practically disappeared. A considerable drop in air temperature immediately following this rise resulted in a corresponding drop in the soil temperatures, but owing to the fact that the sod covering in one instance slowed down evaporation, a difference in the temperature gradient resulted. This was most noticeable on the 25th of the month, when there was a difference of 4° in the temperature spread of the two situations. The bare ground, allowing of quicker evaporation, was colder.

During the spring months it will be noticed that any fairly heavy rainfall is followed by a narrowing of the temperature gradient in the soil. Even in midwinter a sharp thaw acts similarly even though the ground be frozen below the 2-foot level. In January from the 6th to the 13th the air temperature was above 0° C. and by the 12th there were water puddles everywhere from the melting snow. (Fig. 7.) The narrowing of the temperature gradient in the sod-covered ground is not striking but is evident nevertheless. The very noticeable effect on the bare-ground graph for this month may not be typical, as one corner of the plot was inundated, but similar conditions prevailed in every hollow and depression in the cultivated fields. Therefore, the introduction of free water in the form of melting snow or rain will cause a sudden sharp rise in soil temperature to the depth affected. This is again demonstrated in the graph for March (fig. 10) where heavy rain reduced the temperature spread in the first 2 feet to less than 0.5°. The effect of such comparatively rapid temperature changes on hibernating organisms is problematical.

THE CONDUCTIVITY OF SOILS OF DIFFERENT TYPES

It was desired to ascertain how the type of the soil affects its conductivity. Four types of soil having widely different characteristics were chosen. These were (1) a sandy loam from the experimental plot where these investigations were carried on; (2) a pure sand from the river bottom; (3) a silt loam from the experimental farm plots, and (4) a peat from the peat bogs of northern Minnesota. As these soils were so different in their physical properties and consequently in their water-holding capacity, the first question which arose was how to handle them so that the results of these conductivity experiments would be comparable. On the suggestion of C. O. Rost, of the division of soils of the Minnesota station, the writer used the

moisture equivalent [4] as a basis of comparison of the temperature results. The moisture equivalent for each soil was determined to be as follows: Sandy loam, 7.39 per cent; river-bottom sand, 2.02 per cent; silt loam, 15.07 per cent; peat, 189.76 per cent.

Owing to faulty technic the results of this series of experiments were negligible and the experiments are mentioned merely to show the basis on which the work was conducted. Subsequent experiments at the Montana Agricultural Experiment Station indicate that the differences in soil conductivity are small. In those tests no attempt was made to control soil moisture. Holes of about a cubic yard capacity were dug in the ground outside and these were filled with loam, sand, and a sticky gumbo,[5] respectively.

Daily temperature readings throughout the months of October, November, and December showed that the greatest difference ob-

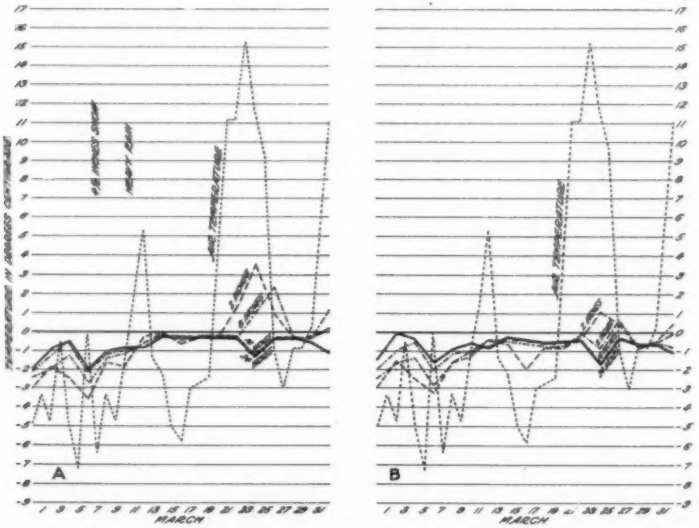

FIGURE 10.—Air temperatures and soil temperatures at different depths in bare (A) and sod-covered (B) ground in March

tained in the temperatures of the three soils at similar levels below 8 inches in depth was in no case greater than 2.2° C. (Tables 1, 2, 3.) The surface layers did show a larger spread, but this, from the standpoint of hibernating organisms, was not significant. A soil-temperature graph (fig. 11) for the period when the lowest temperatures prevailed at Bozeman, Mont., i. e., from January 15 to February 15, shows very clearly the slight differences between the temperatures of gumbo and sand at the same levels. Since moisture plays so important a rôle in the conductivity of the soil, very different results may be anticipated from a similar experiment in which soil is used at the moisture equivalent, but the conditions described are such as would be found in the field and are probably a more reliable indication of what one might expect to find in nature.

[4] The amount of water the soil will hold against a force of 1,000 times gravity.
[5] A fine colloidal clay containing practically no humus.

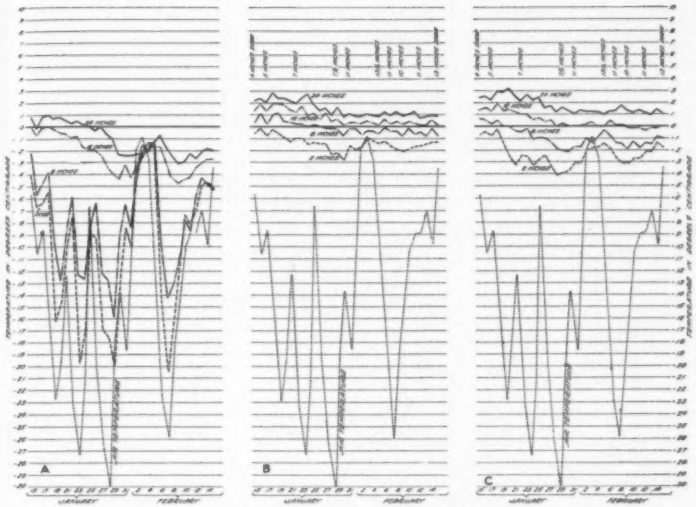

FIGURE 11.—Air temperatures and soil temperatures at different depths in bare ground (A), snow-covered gumbo (B), and snow-covered sand (C) at Bozeman, Mont., during the coldest part of the year

TABLE 1.—*Daily temperature readings (°C.) of different types of soils at different depths recorded during part of October at Bozeman, Mont., as compared with air temperatures*

Date	2-inch depth			8-inch depth			16-inch depth			24-inch depth			Air temperature
	Loam	Gumbo	Sand	Loam	Gumbo	Sand	Loam	Gumbo	Sand	Loam	Gumbo	Sand	
Oct. 11	1.9	3.8	3.3	7.0	8.2	7.3	10.2	10.2	10.3	10.8	10.9	11.4	2.8
Oct. 12	0	.7	.8	3.8	5.0	4.1	7.8	7.6	7.2	8.5	8.5	9.1	2.3
Oct. 13	.2	.5	.7	3.7	4.6	3.7	8.2	7.8	7.2	8.7	9.3	9.3	2.5
Oct. 14	2.7	3.6	4.6	4.5	5.6	5.2	8.8	7.7	7.6	9.8	9.0	9.2	3.5
Oct. 15	3.4	4.2	4.6	4.7	5.6	5.7	7.9	7.7	7.8	9.0	9.0	9.6	4.2
Oct. 16	4.2	4.1	4.3	5.0	5.6	6.0	7.3	6.9	7.9	8.0	7.8	9.1	4.6
Oct. 17	9.9	7.4	8.3	8.0	8.0	8.8	9.3	8.7	9.4	9.3	9.3	10.0	5.0
Oct. 18	2.3	3.2	3.4	5.6	6.4	6.4	7.6	7.1	8.1	8.0	7.4	8.5	4.4
Oct. 19	2.3	4.3	4.8	7.2	8.1	8.1	9.4	9.3	9.9	9.6	9.3	10.3	4.9
Oct. 20	5.3	5.3	6.2	7.5	7.5	7.6	9.2	7.7	8.7	9.5	8.2	9.0	4.7
Oct. 22	3.0	4.3	5.0	4.0	4.3	4.5	7.25	6.0	6.6	8.0	7.5	7.5	4.6
Oct. 23	5.3	4.6	4.5	6.0	6.1	6.5	8.0	7.6	8.5	8.2	8.3	8.9	5.0
Oct. 24	3.5	3.3	3.4	5.6	6.5	6.5	7.8	7.6	8.0	7.9	7.5	8.1	4.4
Oct. 25	3.2	2.9	3.5	5.1	6.1	6.1	7.6	7.3	7.8	8.2	8.0	8.6	4.5
Oct. 26	1.6	2.6	3.0	5.2	6.2	6.4	7.6	7.3	8.2	8.1	8.2	9.0	4.5
Oct. 28	1.3	2.0	2.0	3.6	5.1	5.8	7.4	7.0	8.1	8.3	8.0	9.3	3.2
Oct. 29	−.2	.6	1.2	3.0	4.3	4.7	7.0	6.8	6.9	7.7	7.7	8.3	3.5
Oct. 30	0	1.4	1.5	3.7	4.5	4.8	7.0	6.5	6.8	7.8	7.5	8.3	3.1
Oct. 31	1.0	2.6	2.5	4.0	5.0	5.0	7.4	7.0	7.1	8.1	7.8	8.6	2.7
Average	2.83	3.23	3.55	5.11	5.93	5.96	8.04	7.57	8.00	8.60	8.38	9.06	3.91

TABLE 2.—*Daily temperature readings (°C.) of different types of soils at different depths recorded during the month of November at Bozeman, Mont., as compared with air temperatures*

Date	2-inch depth			8-inch depth			16-inch depth			24-inch depth			Air temperature
	Loam	Gumbo	Sand	Loam	Gumbo	Sand	Loam	Gumbo	Sand	Loam	Gumbo	Sand	
Nov. 1	−1.2	0	1.0	3.1	4.0	4.4	6.9	6.3	6.7	7.8	7.4	8.2	2.1
Nov. 2	−3.1	−1.0	−.9	1.2	2.9	2.3	5.1	5.2	5.1	7.0	6.6	7.0	2.2
Nov. 3	−1.3	0	.3	2.1	3.2	3.0	6.0	5.6	5.4	7.0	6.8	7.5	2.9
Nov. 5	1.1	1.8	2.2	2.6	3.7	4.2	5.7	5.3	6.3	6.8	6.8	7.8	3.6
Nov. 6	1.0	2.1	2.0	2.6	3.3	3.5	4.8	4.7	5.0	6.0	5.7	6.8	3.6
Nov. 7	−1.1	.7	1.2	2.0	3.2	3.7	5.0	4.7	5.2	5.2	5.4	6.4	3.2
Nov. 8	−1.0	.2	1.1	1.5	2.7	3.0	4.2	4.5	4.9	5.1	5.3	6.0	3.5
Nov. 9	0	1.4	1.6	1.6	2.7	3.1	3.9	3.8	5.0	4.9	4.7	6.2	4.0
Nov. 10	4.9	4.2	4.8	4.8	4.8	5.2	5.6	5.4	5.9	6.2	6.0	6.9	4.8
Nov. 11	1.3	2.5	2.3	4.0	4.5	5.8	5.9	5.3	6.5	6.3	6.0	7.4	4.0
Nov. 12	−.2	2.1	2.0	3.0	3.8	4.7	4.9	4.9	6.0	5.6	5.1	6.8	4.5
Nov. 13	5.0	4.9	5.6	5.3	5.1	5.9	5.8	5.4	6.6	6.0	5.8	7.1	4.7
Nov. 14	1.3	3.1	2.5	4.0	4.8	5.3	5.8	5.5	6.6	6.0	6.0	7.2	3.6
Nov. 15	3.7	2.8	2.8	2.8	4.1	4.3	5.4	5.7	5.5	6.2	6.0	6.3	3.5
Nov. 16	0	1.2	1.2	2.8	4.2	3.8	5.7	5.3	5.5	6.1	6.1	6.5	3.0
Nov. 17	.7	1.7	1.6	2.2	3.8	3.3	5.4	5.3	5.0	6.2	6.2	6.4	2.6
Nov. 18	.2	.1	.9	2.5	2.5	2.7	5.0	4.7	4.2	5.4	5.2	5.5	1.6
Nov. 19	0	.3	.8	1.7	2.8	2.7	4.5	4.7	4.5	5.3	5.3	6.0	2.6
Nov. 20	0	1.0	1.0	1.9	2.7	2.7	4.3	4.3	4.4	5.3	5.3	5.9	3.3
Nov. 21	.3	.4	.8	2.1	2.7	2.1	4.4	4.4	4.2	5.2	4.9	5.5	3.9
Nov. 22	.8	.8	1.0	2.7	3.0	3.0	4.6	4.0	4.5	5.4	4.8	5.5	4.1
Nov. 23	.2	.5	1.2	2.3	3.3	3.2	4.1	4.3	4.6	4.9	5.3	5.6	4.0
Nov. 24	.4	.7	1.3	2.9	3.2	3.1	4.8	4.8	4.3	5.3	5.2	5.9	3.5
Nov. 25	1.2	1.8	1.2	1.7	2.3	2.5	4.1	3.7	4.2	5.0	4.6	5.3	3.6
Nov. 26	.6	1.3	1.2	2.3	3.9	3.0	4.5	4.6	4.6	5.2	5.1	5.6	3.8
Nov. 27	0	1.0	.9	1.8	3.0	2.8	4.5	4.7	4.8	5.2	5.0	5.9	2.9
Nov. 28	0	.5	.6	1.7	2.7	2.4	4.0	4.5	4.3	4.8	4.9	5.9	1.9
Nov. 29	−.7	−.2	0	1.0	1.8	2.1	3.5	3.6	3.7	4.4	4.4	5.1	1.5
Nov. 30	−.7	−.3	.3	1.2	1.8	1.8	3.3	3.5	3.7	4.3	4.2	4.8	2.0
Average	.462	1.22	1.46	2.46	3.22	3.43	4.88	4.78	5.07	5.65	5.52	6.31	3.29

TABLE 3.—*Daily temperature readings (°C.) of different types of soils at different depths recorded during the month of December at Bozeman, Mont., as compared with air temperatures*

Date	2-inch depth			8-inch depth			16-inch depth			24-inch depth			Air temperature
	Loam	Gumbo	Sand	Loam	Gumbo	Sand	Loam	Gumbo	Sand	Loam	Gumbo	Sand	
Dec. 1	0	0	0	1.5	2.0	1.5	3.7	3.7	3.3	4.3	4.3	4.8	2.5
Dec. 2	−.2	−.1	−.1	.2	.1	.1	.6	.6	.5	.6	.7	.8	1.8
Dec. 3	−1.3	−.4	−.3	.6	1.3	1.4	3.1	3.0	3.0	3.8	3.9	4.3	.8
Dec. 4	−3.1	−.7	−1.3	.5	1.2	1.2	3.3	3.0	3.0	3.8	3.7	4.2	.6
Dec. 5	−2.8	−.6	−1.3	0	1.3	.8	2.8	2.9	2.8	3.3	3.6	4.2	1.6
Dec. 6	−3.4	−.6	−1.4	−.4	1.4	.9	2.8	3.0	2.7	3.8	3.8	4.3	1.8
Dec. 7	−4.9	−.7	−1.9	−.9	1.2	.7	2.7	2.3	2.4	3.3	3.3	4.0	2.3
Dec. 8	−2.0	.3	0	.6	2.5	2.1	4.3	4.2	4.3	4.8	4.8	5.7	2.8
Dec. 9	−4.0	−1.8	−2.4	−1.9	0	0	1.1	1.0	1.0	1.7	1.6	1.6	3.0
Dec. 10	−3.7	−1.4	−2.3	−1.3	0	0	1.3	1.4	1.3	2.9	2.5	3.0	3.2
Dec. 11	−1.0	−.6	−.3	−.4	.3	.5	2.1	2.2	2.0	3.0	2.8	3.6	3.1
Dec. 12	−1.4	−.4	−1.5	.4	1.1	.2	2.7	2.4	2.0	3.2	3.2	3.9	1.6
Dec. 13	−.8	0	0	1.0	2.2	2.0	3.6	3.3	3.3	4.6	4.2	4.9	1.7
Dec. 14	−2.1	−.9	−1.1	−.9	.1	0	1.3	1.3	1.8	2.1	2.6	3.1	2.3
Dec. 15	−2.2	−1.0	−1.0	−1.0	0	0	1.1	1.2	1.2	2.3	2.3	2.6	1.8
Dec. 16	−1.4	−.9	−.7	−.7	.2	.1	1.5	1.5	1.4	2.3	2.5	3.1	1.6
Dec. 17	−1.7	−.8	−.8	−.6	.3	0	1.5	1.6	1.5	2.3	2.3	2.6	1.3
Dec. 18	−1.4	−.6	−.4	−.3	.4	.3	1.7	1.9	1.8	2.4	2.5	3.2	1.4
Dec. 19	−1.2	−.2	−.3	0	.8	.9	2.2	2.2	2.1	3.1	3.0	3.5	1.2
Dec. 20	−.3	−.1	−.2	.2	.9	.8	2.2	2.1	2.1	2.9	2.8	3.5	1.6
Dec. 21	−1.6	−.7	−.9	−.5	.3	.1	1.7	1.3	1.3	2.5	2.4	2.9	1.9
Dec. 22	−2.6	−.8	−.9	−.5	.2	0	1.7	1.4	1.5	2.3	2.3	2.8	2.2
Dec. 23	−3.0	−1.4	−1.3	−1.4	−.5	−.5	1.2	1.2	1.0	2.0	2.1	2.4	1.9
Dec. 24	−2.3	−.7	−1.1	−.8	.3	.2	1.9	1.5	1.5	2.3	2.4	2.8	1.8
Dec. 25	−1.3	−.7	−.5	−.4	.3	.2	1.4	1.6	1.7	2.2	2.3	3.0	3.0
Dec. 26	−2.3	−.7	−.7	−.6	.3	0	1.2	1.3	1.3	2.1	2.0	2.6	2.3
Dec. 27	−1.0	−1.0	−.3	−.4	.1	0	1.5	1.5	1.3	2.1	2.2	2.5	4.0
Dec. 28	0	−.9	0	−.3	0	.3	1.3	1.1	1.6	1.9	1.8	2.8	3.6
Dec. 29	.8	0	.5	1.2	.6	1.0	2.5	1.8	2.0	2.9	2.7	3.3	3.1
Dec. 30	1.2	0	.3	1.1	.7	.7	2.3	1.8	1.7	2.8	2.5	3.0	2.9
Dec. 31	.9	.5	.9	1.3	1.4	1.3	2.7	2.4	2.6	3.2	3.2	3.7	2.0
Average	−1.61	−.57	−.687	−.5	.671	.54	2.09	1.99	1.96	2.8	2.78	3.31	2.15

Bouyoucos (*1*) showed that there is a remarkable equality in the specified heats of diverse types of soils and that this factor exercises practically no influence in causing and maintaining a difference in temperature in these various soils. It is the water content of the soil which is probably one of the chief intrinsic factors which might affect temperature variations. The average temperature of diverse classes of soils is not so variable as is popularly believed, and the well-known influence of color in affecting soil temperature is not here considered, as this factor can be largely discounted in winter on account of the snow.

INSECT SURVIVAL AT VARIOUS LOW TEMPERATURES

EFFECT ON WIREWORMS OF SUDDEN LOWERING OF TEMPERATURE

Many insect groups which are winter hardy have been found to have a lower freezing point in winter than they have in summer; in other words, they are able to withstand exposure in winter to temperatures which in summer would kill them. Payne (*13*) summarized the work done in this field by several workers, and demonstrated that the freezing point of oak borers becomes lower in winter and rises in the spring, and by summer is very near to that of water.

On July 17 several well-grown larvae of *Melanotus communis* Gyll. and *Ludius aeripennis*, Kirby var. *tinctus* were collected in the field and placed at a constant temperature of 5° C. At the end of 60 days one-third of these were dead, the remainder being still apparently healthy and active when the temperature was raised. A second batch of larvae of both species collected in summer and placed at a temperature of between 0° and 2° were all dead at the end of 14 days. This mortality was probably due to the fact that they were collected in summer, and, without being allowed to harden off by being submitted to a gradual lowering of the temperature, were placed immediately at a subnormal temperature for that time of the year. Since the mortality at 5° was so much smaller than at 0° to 2° it would appear that a range of a very few degrees above freezing is a critical point.

FREEZING POINT OF WIREWORMS IN LABORATORY EXPERIMENTS

Payne established the fact that wireworms (*Elater* sp.) are among the insects which undergo a hardening process. She noted that there is a considerable variation in the freezing points of individuals of any given species at a given time, or a periodicity in the freezing and undercooling points of the same species. This is borne out by the death of wireworms exposed suddenly to the relatively high temperature of 2° C. Gradual chilling, a few degrees at a time, results in the acquirement of a hardiness which enables the insect to withstand extremes of cold, and Payne shows that the average freezing point of several larvae of the wood-borer, *Synchroa punctata*, chilled at −3° is decidedly lower than that of individuals of the same species which had not been chilled.

Using the technic described by Payne, the writer determined the freezing points of *Melanotus communis* larvae and adults. The hardening-off process apparently does not become pronounced until after exposure of the insect to temperatures lower than 8° C. This assumption is based on the fact that larvae which had been held at

constant temperatures of 32°, 27°, 22°, 17°, 12°, and 8° for some weeks showed little difference in their freezing and undercooling points. Also, the summer-collected larvae kept at 0° to 2° C. were all dead in 14 days. Of those kept at 5° approximately 66 per cent survived and among those kept at 8° there was no mortality.

TABLE 4.—*Effect upon freezing and undercooling points of holding Melanotus communis larvae at different constant temperatures for some weeks*

Larvae held at—	Average undercooling point of six larvae	Average freezing point for six larvae
°C.	°C.	°C.
32	−3.28	−0.79
27	−6.6	−.96
22	−6.36	−1.21
17	−7.11	−1.44
12	−7.33	−1.35
8	−5.93	−.99

The freezing points (shown in Table 4) were obtained by the piercing method, i. e., by puncturing the insect with the sharpened end of a thermojunction which was then forced into the tissues. The temperatures obtained seemed hardly logical in view of the conditions experienced by these larvae in nature and, in agreement with Carter (*3*), were not considered reliable. By the contact method, holding the couple in close contact with the insect, an average undercooling point of −14.6° C. and a freezing point of −12.8° were obtained. The averages by the piercing method were −6.1° and 1.11°, respectively.

The probable reason why freezing-point determinations made by the piercing method are unreliable is explained by Robinson (*16, p. 751*), as follows:

> * * * When an insect is pierced a shock is produced within the organism which is accompanied by a flooding of the tissues with free water, due probably to the release of bound water held by the cell colloids. As a result, the lymph becomes diluted and the freezing point is raised.

In order to verify the possible accuracy of the piercing and contact methods, the following experiment was conducted. Several Melanotus larvae were placed in a Carrier temperature cabinet at a temperature of −2° C. Every 48 hours the temperature was lowered by 2 degrees, and at these times a larva was sectioned and examined microscopically for ice crystals. It was found that not until a temperature of −12° was reached were ice crystals present, which is in agreement with the freezing point of −12.8° determined by the contact method.

Similar discrepancies having been observed in determining the freezing points of the adult, a visual check was likewise run on 21 individuals. For the adults, by the piercing method, the average undercooling point was found to be −6.92° C. and the freezing point −3.16°. By the contact method the average undercooling point was −18.3° and the freezing point −15.5°. A correlation chart, such as is described by Robinson (*16*), was prepared for the adults of *Melanotus communis* to enable an approximation to be made of the natural undercooling and freezing points by contact. By using the figures −18.3 as the undercooling point and −15.5° as the freezing

point observed by the contact method, the chart shows the natural internal undercooling point to be −17.8° and the internal freezing point to be −14.8°. Several beetles from the same lot were, like the larvae, placed in the low-temperature cabinet and individuals removed at intervals for examination. The abdomen was cut in two with a pair of previously chilled scissors, and the tissue quickly examined under a binocular microscope. If the tissues were still fluid, the temperature in the cabinet was lowered by another degree. Observations are recorded in Table 5.

TABLE 5.—*Effect of exposure to low temperatures for a period of six hours upon the adults of Melanotus communis*

Temperature	Result
°C.	
−11	No sign of freezing.
−12	Do.
−13	Do.
−14	Do.
−16	Tissues frozen.

The beetles used in these tests apparently froze between −14° and −16° C., this being in close agreement with the internal freezing point as determined by the correlation chart. Several beetles were removed from the cabinet after 12 hours' exposure of −16° and allowed to thaw out at room temperature. In less than four hours they recovered their normal activity. A further series of temperature decreases to which the remaining beetles were subjected showed that they were able to withstand temperatures much lower than their undercooling point.

TABLE 6.—*Ability of adults of Melanotus communis to recover their normal activity after exposure to low temperatures for different periods of time*

Temperature	Period of exposure	Result
°C.	*Hours*	
−17	7	Recovered in less than six hours.
−18	12	Do.
−19	12	Do.
−21	12	Do.
−23	8	Did not recover.
−24	12	Do.

It would thus appear that the freezing point of *Melanotus communis* larvae is about −13° C. and that of the adults about −15°.

In this connection it is interesting to note that Fulton (*6*), working with the same species, found that the larvae were more resistant to heat than the adults, although, as stated above, the larvae are less resistant to cold.

FREEZING POINT OF WIREWORMS IN OUTDOOR CAGES

In connection with these hibernation studies it was desired to ascertain the freezing points of both adults and larvae of wireworms. As a preliminary to these freezing-point determinations, several larvae and adults of two species of wireworms, *Ludius aeripennis*, var.

tinctus and *Melanotus communis*, were buried at 2-inch intervals in the ground near the buried thermocouples. These wireworms were placed in salve tins previously well perforated with numerous small holes and filled with damp sand. Four cans were placed at each 2-inch interval from 2 to 24 inches in the fall of 1927 and dug up for examination on May 27, 1928. On examination it was found that the mortality was very low and obviously not due to temperature conditions. Of 49 larvae buried in the fall, 43 were found to be alive and active when dug up. The only beetle found dead was in a cage at the 4-inch level, the larvae in this cage also being dead, so probably their deaths were due to some local condition within the cage, as both adult and larvae at the colder 2-inch level survived. The dead larvae were from cans buried at depths of 4, 6, 10, and 12 inches, there being no deaths of either beetles or larvae at 2 inches. In the case of the 6 and 12 inch fatalities there were ants present and the larvae had been devoured, only the chitinous exuvium being left. However, it is improbable that the ants had killed the wireworms. All of the beetles which survived lived in the laboratory until the middle of July when they commenced to die off for want of attention. For food they were supplied with honey sirup.

Inasmuch as the lowest temperature to which these insects were exposed at 2 inches under snow was only −14.3° C. on January 28, and to that temperature but for one day, no mortality directly attributable to low temperature was to be expected.

McColloch, Hayes, and Bryson (*11*) in making hibernation studies on white grubs in Kansas, found that only 11.2 per cent of the 1,188 white grubs dug up were above the 6-inch level. Between 6 and 12 inches, 42 per cent were found, making 53.2 per cent of the grubs hibernating in the first 12 inches. Below the 24-inch level only 3.8 per cent were found.

H. L. Sweetman, working in Minnesota, found that white-grub adults have a much higher freezing point than wireworms. In beetles collected from the field on October 30, when presumably they had been subjected to some weeks of hardening, he found the undercooling point (by the contact method) to be −10.58° C. and the freezing point −6.5°. The average temperatures for several white-grub beetles with different previous histories were undercooling point −6.94° and freezing point −3.28°. In Table 7 are presented Sweetman's data (unpublished) showing the ability of June bugs, *Phyllophaga implicita*, to withstand low temperatures in their natural environment.

TABLE 7.—*Ability of June bugs to withstand low temperatures when at various depths in the soil*

Depth in soil	Number of adults—		Number of grubs—		Lowest temperature
	Alive	Dead	Alive	Dead	
Feet					° *C.*
0.5	0	9	0	2	−8.0
1.0	1	9	0	2	−6.75
1.5	3	7	0	2	−5.25
2.0	7	3	0	2	−3.75
4.0	10	0	1	1	0
5.0	10	0	2	0	0
6.0	6	4	2	0	0

It will be readily seen from these data that white grubs must of necessity hibernate at much lower depths than wireworms if they are to survive winter soil conditions, on account of their higher freezing points.

The freezing point of the larvae is not definitely known. It is apparently not much below 0° C. and in southern Minnesota they would, even under snow, have to go below 2 feet to overwinter successfully. Criddle (*5*) in Manitoba, records finding grubs which were hibernating at much greater depths than those recorded by McColloch and Hayes in Kansas (*9*). From this it would appear that as one proceeds northward into colder climates the white grubs will be found hibernating at greater depths, and in southern Minnesota one would expect to find them at depths intermediate between those recorded from Kansas and Manitoba. If this be the case, then it would be conservative to assume that the majority of the Minnesota white grubs hibernate below 2 feet in depth. On this assumption, during the period of this study the minimum temperature to which they would have been exposed was above −6.9°, and under Minnesota conditions they would have adequate protection even in the entire absence of snow.

Normally the majority of wireworms, both adults and larvae, hibernate from 4 to 7 inches, although McColloch, Hayes, and Bryson (*10*) show them as ranging from 3 to 36 inches, the majority being found at 7.7 inches during one winter and 10.1 inches during another. It has, however, been the observation of the writer, both in Alberta and Minnesota, that wireworms most often enter hibernation at a depth of from 5 to 7 inches. Be that as it may, wireworms, with their ability to withstand great extremes of temperature, will be amply protected from all danger of freezing in this latitude. Again referring to this season's temperature studies, it is apparent that even those wireworms which had entered into hibernation at a depth of 4 inches would only have experienced a minimum temperature of −17.8° C. which would probably be still within the safety zone for adults. This temperature would undoubtedly prove fatal to such of the larvae as were caught at 4 inches, their undercooling point being about −14.6° C., but those which were present at greater depths, and they are normally in the majority, would survive even bare-ground temperatures. Even as little as half an inch of snow affords sufficient assurance that the larvae will survive a normal Minnesota winter. It would require a prolonged spell of temperature in the neighborhood of −20 °F. with an entire absence of snow, to destroy the wireworm population to any extent.

TO WHAT EXTENT DOES TEMPERATURE CONTROL WIREWORMS?

Wireworms do not build up and by their increase annually widen an area of infestation. Their long life cycle, from 3 to 5 years, if not longer, means slow multiplication. Infestations as a rule are local in character. A severely infested field or two may be found in one district and the nearest other infestation of importance may be many miles distant. This localization is, in the case of species the adults of which do not fly, e. g., *Ludius aeripennis* Kby., partly due to their restricted powers of locomotion. But some species are strong fliers and some other reason must be looked for to explain the

marked fluctuation in the incidence of this pest. Their known enemies are few. With few excepting predacious larvae and ground beetles can not, except in the case of very immature wireworms, pierce their thick chitinous cuticle. Some large Calosoma beetles, starved for several days and then liberated in a cage with several wireworms, avidly seized half-grown larvae in their mandibles but were unable to make the slightest impression. In the rearing cages fungous diseases attack the wireworms occasionally. A few worms in the laboratory died of a disease identified as *Oospora destructor* (Metch) Delacr. and healthy worms brought into contact with the diseased were also attacked and killed. Adults in the oviposition cages were killed by this same fungus. But the percentage of larvae or adults observed so killed in nature is infinitesimal. As to parasites, the only case which has come to the attention of the writer is an instance mentioned by Lane, who once obtained an unidentified parasite from a wireworm. Thomas (*19*), after a thorough review of the literature on parasites of wireworms, lists only 19 cases of insect parasitism and four annelid parasites, many of the observations not being well authenticated. On one or two occasions mites of the family Tyroglyphidae have been observed heavily infesting wireworms, but the hosts did not appear to be unduly inconvenienced apart from the mechanical irritation induced by their presence. Mite-infested wireworms have been kept for months and they developed normally and finally pupated. These are probably merely cases of indirect phoresy such as is mentioned by Wheeler (*20*). Bacterial disease undoubtedly takes a considerable toll of both wireworms and pupae, especially the latter. Dead and flaccid worms have been dug up occasionally, as well as several pupal cells containing a disintegrating mass. Birds, too, play their part in keeping down the number of wireworms, picking up many behind the plow. Pomerantezev (*14*) dissected out the stomachs of 120 rooks and found that insect pests and their larvae occurred to the extent of 55 to 76 per cent. Two species of wireworms, *Agriotes* and *Ludius*, were well represented among other beetles.

Climatic conditions then must undoubtedly be a control factor of much importance. In the summer when the larvae are active they can go down to escape fatal high temperatures, but as the soil cools they become dormant and a further drop in temperature after they become inactive finds them unable to escape. If the cold weather at this time is severe and sufficiently prolonged many of the wireworms will not survive. To a certain extent then, one may prognostigate from a study of the climatic conditions during the winter months whether such a pest as the wireworm is likely to be more, or less, severe during the ensuing spring. Wireworms are, according to King (*8*) among the major pests in Saskatchewan, and undoubtedly the heavy snowfall affords ample protection against the subzero weather which prevails for long intervals during most of the winter months in that Province. But it is not outside the bounds of possibility that a cold spell of several days' duration might follow a chinook,[6] and under such circumstances a heavy wireworm mortality might reasonable be expected.

[6] A warm sustained southwest wind common in parts of western North America, and which during the winter causes a rapid rise in temperature and removes all snow.

SUMMARY

A thermocouple apparatus for taking soil temperatures is described.

Records of soil temperature during the winter months in Minnesota at depths from 2 to 24 inches are analyzed.

Snow is normally an adequate protection from cold to insects which hibernate at depths below 4 inches.

Rain or a rise in temperature inducing a thaw destroys the temperature gradient in the first 2 feet, and if such conditions are followed by a decided drop in temperature, hibernating insects may suffer high mortality.

The differences in the conductivity of soils of various types are not sufficiently great to be significant in insect hibernation.

Larvae and adults of *Melanotus communis* have a sufficiently low freezing point to withstand Minnesota winter temperatures if they hibernate below 4 inches in the ground.

Larvae and adults of two species of wireworms buried outside all winter at depths from 2 to 24 inches practically all survived—the small mortality not being due to temperature conditions. The possibility of larvae and adults of white grubs surviving similar conditions is discussed.

It is concluded that winter climatic conditions may in certain instances cause heavy mortality among hibernating wireworms.

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RELATION OF SIZE OF SWINE LITTERS TO AGE OF DAM AND TO SIZE OF SUCCEEDING LITTERS[1]

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INTRODUCTION

The objects of this investigation were two: (1) To determine the relation of size of swine litter produced at a given age of the mother and the size of litters produced at later ages, and (2) to ascertain the relation of the size of a given litter to that of succeeding litters.

SOURCE OF MATERIAL

The data for this study were taken from the breeding and farrowing records of the swine herd of the department of animal husbandry of the University of Illinois, accumulated during the years 1903 to 1925. This investigation includes 935 litters containing 8,478 pigs of 7 breeds. The records were kept by the herdsmen actively in charge of the barns. The temporary records of the herdsmen were transferred to permanent records in the office, and from these the data for this study were taken. The breeds involved are Duroc-Jersey, Berkshire, Poland China, Chester White, Hampshire, Yorkshire, and Tamworth. The Duroc-Jersey, Berkshire, and Poland China comprise 24.4 per cent, 31 per cent, and 20.7 per cent, respectively, of the total number of litters studied. (Table 1.)

TABLE 1.—*Number of pigs, number of litters, and average size of litters studied*

Breed	Number of pigs	Number of litters	Average size of litter	Breed	Number of pigs	Number of litters	Average size of litter
Duroc-Jersey	2,265	228	9.93	Hampshire	472	52	9.07
Berkshire	2,442	290	8.42	Tamworth	455	45	10.11
Poland China	1,536	194	7.91				
Chester White	794	81	9.80	Total	8,478	935	9.06
Yorkshire	514	45	11.42				

OUTLINE OF THE STUDY

The litters were grouped into classes on the basis of the age of the dam, and the dams were classified on the basis of age at the time of farrowing, in intervals of six months, as follows: 10–15, 16–21, 22–27, 28–33, 34–39, 40–45, 46–51, 52–57, and up to 94–99.

The different phases of the study are as follows:

(1) The relation of the size of litter to the age of dam is shown for Duroc-Jersey, Berkshire, and Poland China breeds separately and for all three combined. (Fig. 1 and Table 2.)

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[2] The author is indebted to Dr. E. Roberts for helpful suggestions during the progress of this study.

(2) The average size of litter produced throughout the lifetime of the sow when first bred at an early age, and the average size of litter produced when the sow was first bred at a later age are shown for the three breeds separately and for the three breeds combined. (Table 3.)

(3) The correlation between the size of litter at a given age of the dam and the size of litter at later ages is shown for Duroc-Jersey, Berkshire, and Poland China breeds separately and for all the seven breeds combined. (Table 4.)

(4) The correlation between the size of one litter and the size of succeeding litters is shown for Duroc-Jersey, Berkshire, and Poland China breeds separately and for all the seven breeds combined. (Table 5.)

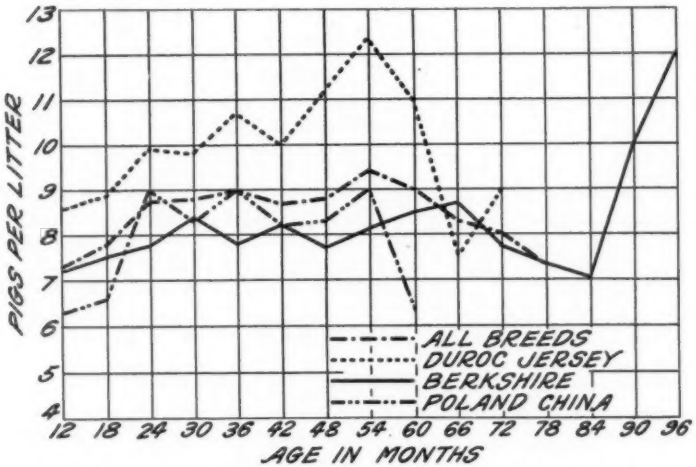

FIGURE 1.—Size of litter farrowed at different ages of the sow. The figures on the abscissa represent average ages; for example, 12 represents the age of sows from 10 to 15 months, inclusive; 18, the age of sows from 16 to 21 months, inclusive

(5) The correlation between the size of the first litter and the average size of the combined second, third, and fourth litters produced by the same individual is shown, and also the correlation between the size of the first and the average size of the combined third and fourth litters produced by the same individual.

(6) The correlation between the size of the second litter and the average size of the combined third and fourth litters produced by the same individual is shown, and also the correlation between the size of the second litter and the average size of the combined third, fourth, and fifth litters produced by the same individual.

TABLE 2.—*Data showing relation between age of dam and size of litter in Duroc-Jersey, Berkshire, and Poland China swine*

DUROC-JERSEY

Age of dam (months)	Number of pigs farrowed	Number of litters	Average size of litter	Age of dam (months)	Number of pigs farrowed	Number of litters	Average size of litter
12	309	36	8.58	48	113	10	11.30
18	312	35	8.91	54	62	5	12.40
24	435	44	9.89	60	44	4	11.00
30	246	25	9.84	66	15	2	7.50
36	235	22	10.68	72	9	1	9.00
42	130	13	10.00				

BERKSHIRE

12	344	48	7.17	60	51	6	8.50
18	331	44	7.52	66	35	4	8.75
24	471	61	7.72	72	31	4	7.75
30	312	37	8.43	78	22	3	7.33
36	266	34	7.82	84	27	1	7.00
42	163	20	8.15	90	22	2	10.00
48	146	19	7.68	96	12	1	12.00
54	81	10	8.10				

POLAND CHINA

12	252	40	6.30	42	106	13	8.15
18	145	22	6.59	48	108	13	8.30
24	360	40	9.00	54	45	5	9.00
30	192	23	8.35	60	13	2	6.50
36	180	20	9.00				

DUROC-JERSEY, BERKSHIRE, AND POLAND CHINA, COMBINED

12	905	124	7.30	60	108	12	9.00
18	788	101	7.80	66	50	6	8.33
24	1,266	145	8.73	72	40	5	8.00
30	750	85	8.82	78	22	3	7.33
36	681	76	8.96	84	27	1	7.00
42	399	46	8.67	90	20	2	10.00
48	367	42	8.74	96	12	1	12.00
54	188	20	9.40				

TABLE 3.—*Average size of litters from sows which farrowed first litter at 12 months compared with average size of litters from sows which farrowed first litters at 18 months*

DUROC-JERSEY

Average size of litters when dam is aged (in months)—															Number of litters	Average size of all litters
12	18	24	30	36	42	48	54	60	66	72	78	84	90	96		
8.58	9.11	10.11	9.94	11.40	12.00	11.55	10.33	10.66	6.00	-----	13.00	-----	-----	-----	137	9.92
-----	8.70	9.92	10.86	9.44	11.00	8.00	9.33	13.00	9.50	9.00	-----	4.00	-----	-----	65	9.60

BERKSHIRE

7.17	7.78	8.10	8.35	8.06	9.89	8.90	8.33	8.37	9.00	7.75	7.75	8.00	10.00	12.00	179	8.05
-----	7.41	6.85	8.75	7.37	7.37	7.80	7.60	11.00	8.00	10.00	9.00	7.00	-----	7.00	90	7.51

POLAND CHINA

6.30	6.54	8.81	8.25	9.27	8.44	7.89	9.00	6.00	-----	-----	-----	-----	-----	-----	137	7.74
-----	6.66	8.16	7.00	8.00	5.50	8.33	6.50	7.00	-----	-----	-----	-----	-----	-----	28	7.18

DUROC-JERSEY, BERKSHIRE, AND POLAND CHINA, COMBINED

7.30	7.95	8.95	8.83	9.54	9.96	9.42	9.00	9.00	8.25	7.75	8.80	8.00	10.00	12.00	453	8.52
-----	7.67	8.12	9.16	8.44	8.50	8.00	7.90	11.00	11.33	9.50	9.00	5.50	-----	7.00	183	8.24

TABLE 4.—*Correlation between the size of litter at a given age of the sow and the size of litters at later ages*

DUROC-JERSEY

Age of dam (months)	Number of litters	r	P. E	Age of dam (months)	Number of litters	r	P. E
10–15 and 16–21	19	−0.115	±0.154	22–27 and 28–33	21	+0.483	±0.112
10–15 and 22–27	26	+.462	±.172	22–27 and 40–45	13	+.662	±.105
10–15 and 28–33	16	+.230	±.164	22–27 and 46–51	12	+.395	±.127
10–15 and 34–39	17	−.225	±.155	28–33 and 34–39	17	+.535	±.116
10–15 and 46–51	9	+.612	±.140	34–39 and 40–45	15	+.780	±.068
16–21 and 22–27	23	+.097	±.112	34–39 and 46–51	13	+.500	±.046
16–21 and 28–33	14	+.298	±.164	40–45 and 46–51	11	+.611	±.127
16–21 and 34–39	17	−.089	±.162				

BERKSHIRE

10–15 and 16–21	15	+0.090	±0.172	22–27 and 28–33	23	−0.249	±0.131
10–15 and 22–27	33	+.680	±.117	22–27 and 34–39	25	−.032	±.134
10–15 and 28–33	22	+.0005	±.143	22–27 and 46–51	15	−.194	±.167
10–15 and 34–39	19	+.226	±.148	22–27 and 52–57	10	+.416	±.176
10–15 and 40–45	10	+.201	±.205	28–33 and 34–39	22	−.095	±.142
16–21 and 22–27	22	+.330	±.128	28–33 and 40–45	12	+.409	±.163
16–21 and 28–33	11	−.315	±.183	28–33 and 46–51	13	+.538	±.132
16–21 and 34–39	12	−.019	±.197	34–39 and 46–51	16	+.070	±.165

POLAND CHINA

10–15 and 16–21	13	+0.684	±0.099	16–21 and 22–27	14	+0.651	±0.103
10–15 and 22–27	30	+.472	±.096	16–21 and 28–33	10	−.056	±.212
10–15 and 28–33	15	+.064	±.170	22–27 and 28–33	21	−.343	±.129
10–15 and 34–39	15	−.449	±.137	22–27 and 34–39	11	+.191	±.036

ALL BREEDS COMBINED *

10–15 and 16–21	62	+0.229	±0.080	22–27 and 34–39	92	+0.277	±0.064
10–15 and 22–27	114	+.313	±.055	22–27 and 40–45	52	+.303	±.085
10–15 and 28–33	74	+.125	±.077	22–27 and 46–51	45	+.253	±.097
10–15 and 34–39	81	+.229	±.071	22–27 and 52–57	22	+.508	+.106
10–15 and 40–45	38	+.653	±.063	28–33 and 34–39	73	+.321	±.071
10–15 and 46–51	33	+.115	±.115	28–33 and 40–45	45	+.526	±.072
10–15 and 52–57	17	−.229	±.155	28–33 and 46–51	39	+.477	±.098
16–21 and 22–27	77	+.440	±.062	28–33 and 52–57	21	+.197	±.141
16–21 and 28–33	54	+.363	±.079	34–39 and 40–45	53	+.425	±.085
16–21 and 34–39	46	+.037	±.099	34–39 and 46–51	51	+.415	±.078
16–21 and 40–45	26	+.018	±.130	34–39 and 52–57	24	+.389	±.168
16–21 and 46–51	18	+.396	±.134	40–45 and 46–51	40	+.603	±.067
16–21 and 52–57	11	+.161	±.197	40–45 and 52–57	25	+.294	±.123
22–27 and 28–33	90	+.139	±.069	46–51 and 52–57	23	+.580	±.140

* Duroc-Jersey, Berkshire, Poland China, Chester White, Hampshire, Yorkshire, and Tamworth.

TABLE 5.—*Correlation between the size of one litter and size of succeeding litters*

DUROC-JERSEY

Litters correlated	Number of litters	r	P. E.	Litters correlated	Number of litters	r	P. E.
1 and 2	53	+0.245	±0.087	2 and 5	15	+0.055	±0.173
1 and 3	37	+.280	±.102	2 and 6	10	+.545	±.129
1 and 4	28	+.040	±.127	3 and 4	25	+.381	±.115
1 and 5	19	+.052	±.154	3 and 5	16	+.633	±.101
1 and 6	11	−.016	±.204	3 and 6	12	+.369	±.167
2 and 3	35	+.392	±.096	4 and 5	17	+.442	±.131
2 and 4	25	+.228	±.123	4 and 6	11	−.009	±.203

BERKSHIRE

1 and 2	81	+0.178	±0.073	2 and 6	13	+.617	±.115
1 and 3	44	+.013	±.102	3 and 4	27	+.267	±.120
1 and 4	27	+.361	±.128	3 and 5	20	+.412	±.118
1 and 5	21	−.799	±.523	4 and 5	21	+.087	±.146
1 and 6	13	−.058	+.181	4 and 6	13	+.216	±.180
2 and 3	41	+.117	±.104	4 and 7	9	−.408	±.185
2 and 4	27	+.119	±.124	5 and 6	13	−.311	±.186
2 and 5	19	−.373	±.133				

POLAND CHINA

1 and 2	43	+0.426	±0.084	2 and 4	20	+0.184	±0.099
1 and 3	29	+.418	±.103	2 and 5	12	+.145	±.176
1 and 4	19	+.182	±.150	3 and 4	20	+.163	±.145
1 and 5	11	+.087	±.201	3 and 5	11	+.603	±.133
2 and 3	31	+.450	±.096				

ALL BREEDS* COMBINED

1 and 2	228	+0.341	±0.030	2 and 7	19	+0.445	±0.139
1 and 3	150	+.232	±.052	3 and 4	96	+.367	±.059
1 and 4	94	+.267	±.064	3 and 5	65	+.542	±.059
1 and 5	67	+.238	±.071	3 and 6	42	−.069	±.100
1 and 6	40	+.256	±.099	3 and 7	22	+.306	±.130
1 and 7	22	−.335	±.140	3 and 8	14	+.524	±.136
1 and 8	14	−.144	±.176	4 and 5	65	+.441	±.067
2 and 3	189	+.367	±.042	4 and 6	42	+.022	±.104
2 and 4	93	+.248	±.066	4 and 7	22	+.438	±.130
2 and 5	68	+.155	±.079	4 and 8	13	+.578	±.120
2 and 6	41	+.664	±.058	5 and 6	40	−.065	±.106

* Duroc-Jersey, Berkshire, Poland China, Chester White, Hampshire, Yorkshire, and Tamworth.

ANALYSIS OF DATA

The average size of all litters involved is 9.06 pigs (Table 1), as compared with 8.1 found by Carmichael and Rice.[3] The average size of litter in present work was determined by including litters only from dams that produced more than one, all dams producing only one being eliminated. This fact may account for the higher average found in this study as compared to that reported by Carmichael and Rice.

Rommel,[4] working with registration records, found the average size of litter for Duroc-Jerseys over a period of 10 years (1893–1902) to be 9.26 pigs and the average size of litter for Poland Chinas over

[3] CARMICHAEL, W. J., and RICE, J. B. VARIATIONS IN FARROW: WITH SPECIAL REFERENCE TO THE BIRTH WEIGHT OF PIGS. Ill. Agr. Expt. Sta. Bul. 236, p. 67–95, illus. 1920.

[4] ROMMEL, G. M. THE FECUNDITY OF POLAND CHINA AND DUROC-JERSEY SOWS. U. S. Dept. Agr., Bur. Anim. Indus. Circ. 95, 12 p. 1906.

a period of 5 years (1898–1902) to be 7.52 pigs. In the present investigation the average size of the Duroc-Jersey litters was found to be 9.93 pigs and the average size of the Poland China 7.91.

There is a marked increase in size of litter with increasing age of the dam until about 4½ years. (Fig. 1 and Table 2.) All breeds combined show an increase in size of litter from 7.3 pigs at 1 year to 9.4 pigs at 4½ years, after which there is a gradual decrease to 7 pigs at 7 years.

Carmichael and Rice [5] found that the average size of litters of all breeds combined reached its peak at 3 years instead of 4½ as found in this study. This may be due to the ration and management of the herd, and the selection of more prolific individuals since the work of Carmichael and Rice.

Hammond [6] concludes from an investigation of the number of corpora lutea present in the ovaries and the number of fetuses present in the uteri that the lower fertility of young sows is due to the formation of a smaller number of ova.

Is the average size of litter during the reproductive life of the sow affected by the age at which she is first bred? Data are presented in Table 3 showing the difference in size of litter produced by sows bred at different ages. Since no difference was found among breeds in this respect, records of Duroc-Jerseys, Berkshires, and Poland Chinas were combined. (Table 3.) The litters from sows that produced only one litter are eliminated. The difference is determined between the average size litter of the group that farrowed their first at 12 [7] months and the average size litter of the group that farrowed their first at 18 [8] months. The average of the sows that farrowed their first litter at 12 months was 8.52 pigs, based on 453 litters. An average of 8.24 pigs per litter for the group of sows that farrowed their first at 18 months was obtained, based on 183 litters. The difference 0.28 ± 0.158 is not significant.

Because of the great variation in size of first litters, these were eliminated in determining the difference of the average of each group. An average of 8.98 pigs per litter for the group that farrowed the first litter at 12 months was obtained, based on 329 litters. The average of the group that farrowed their first at 18 months was 8.49 pigs per litter, based on 127 litters. The difference 0.49 ± 0.173 is not significant.

Evidently breeding sows at an early age does not increase their fertility. However, no evidence was found to show that breeding sows as young as possible lowers fertility. On the other hand, early breeding makes possible a greater total number of pigs during the breeding life of the sow and also has the advantage of enabling the breeder to detect barren females earlier than would otherwise be the case.

The number of litters involved in the group in which the litters were farrowed at 2 years of age are so few that no conclusion can be drawn.

In Table 4 are shown coefficients of correlation between the size of litter at a given age of the sow and size of litter at later ages. A

[5] CARMICHAEL, W. J., and RICE, J. B. Op. cit.
[6] HAMMOND, J. ON SOME FACTORS CONTROLLING FERTILITY IN DOMESTIC ANIMALS. Jour. Agr. Sci. [England] 6: [263]-277, illus. 1914.
[7] Farrowed in the interval between 10 and 15 months, inclusive.
[8] Farrowed in the interval between 16 and 21 months, inclusive.

marked correlation ($r = +0.313 \pm 0.055$) is observed between the size of litters farrowed at 1 year and the size of litters at 2 years in which 114 litters are involved.

There is also a significant correlation between the size of litter at 2 years and the size of litter at 4½ years, $r = +0.508 \pm 0.106$; between 2½ and 3½ years, $r = +0.526 \pm 0.072$; between 2½ and 4 years, $r = +0.477 \pm 0.098$; between 3 and 3½ years, $r = +0.425 \pm 0.085$; between 3 and 4 years, $r = +0.415 \pm 0.078$; between 3½ and 4 years, $r = +0.603 \pm 0.067$.

The numbers involved in the correlations between the size of one litter and the size of the succeeding litters in Duroc-Jerseys, Berkshires, and Poland Chinas separately are, in general, too small to be significant. (Table 5.)

Among all breeds a significant correlation is observed. (Table 5.)

Between the first and second litters, $r = +0.341 \pm 0.030$.
Between the first and third litters, $r = +0.232 \pm 0.052$.
Between the first and fourth litters, $r = +0.267 \pm 0.064$.
Between the second and third litters, $r = +0.367 \pm 0.042$.
Between the second and sixth litters, $r = +0.6664 \pm 0.058$.
Between the third and fourth litters, $r = +0.367 \pm 0.059$.
Between the third and fifth litters, $r = +0.542 \pm 0.059$.
Between the fourth and fifth litters, $r = +0.441 \pm 0.067$.
Between the fourth and eighth litters, $r = +0.578 \pm 0.120$.

The correlation between the size of the first litter and the average of the second, third, and fourth with 98 litters involved was found to be $r = +0.232 \pm 0.065$; the correlation between the size of the first litter and the average of the second, third, fourth, and fifth with 67 litters involved was found to be $r = +0.195 \pm 0.079$; the correlation between the size of second and the average of the third and fourth with 98 litters involved was found to be $r = +0.409 \pm 0.059$; and the correlation between the size of second and the average of the third, fourth, and fifth with 67 litters involved was found to be $r = +0.290 \pm 0.075$.

The correlation between the size of the second litter and the average size of succeeding litters is more significant than the correlation between the size of the first and the average size of succeeding litters. The correlation between the size of the first litter and the average size of succeeding litters is less than four times the probable error; while the correlation between the size of second litters and the average of succeeding litters is more than four times the probable error.

The higher coefficient of correlation obtained between the second and succeeding litters is due to the greater variation in the size of first litters. The greater variation in the size of the first litter is clearly shown in the calculation of the coefficients of variability of the first and second litters involved in the correlation. (Table 6.)

TABLE 6.—*Coefficient of variability of the first and second litters*

Litter	Number of litters	Coefficient of variability	Probable error
First	98	36.64	±1.50
Second	98	28.95	±1.39

SUMMARY AND CONCLUSIONS

In general the size of litter increases with the age of the dam up to about 4½ years, after which a gradual decrease occurs.

The fertility of a sow is not affected by the age at which she is first bred, but the results of this investigation show that it is advisable to breed the sow young, since more pigs will be produced throughout her breeding life. Moreover, early breeding makes possible early elimination of barren individuals.

A significant correlation exists between the size of litter farrowed at a given age of the dam and the size of litter farrowed at later ages of the dam.

Where sufficiently large numbers of litters were available for study significant correlations were found between the size of a given litter and the size of succeeding litters.

A high correlation exists between the size of the second litter and the average size of later litters.

The coefficient of variability in size of first litters is greater than in the size of second litters.

This study shows that size of litter is a valuable criterion in selection for fertility.

EFFECT OF CEANOTHUS BRUSH ON WESTERN YELLOW PINE PLANTATIONS IN THE NORTHERN ROCKY MOUNTAINS[1]

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INTRODUCTION

Forest planting in the northern Rocky Mountain region is largely confined to areas that have been burned over twice, the second burning occurring during recent years. Planting crews can operate on these "double burns" with relative ease because the fires have removed shrubs and other obstructions. Unfortunately planting activity on forest lands is not keeping pace with the accumulation of areas denuded by fire, and as time passes these lands rapidly revert to shrubby growth from the uninjured roots of the original bushes and from wind-borne seeds. Released from competition, other than that of herbaceous plants, the bushes frequently usurp the area. This is especially true of *Ceanothus velutinus* on southerly slopes. Certain areas are considered "too brushy to plant" because of the mechanical hindrance of the bushes. On other areas those in charge of this work feel uncertain as to whether or not the beneficial effect of shade from the bushes is greater than the detrimental effect of root competition. Hence, when confronted with a bush in his path, the planter lacks instructions about the proper location of his seedlings. Each planter, therefore, follows the line of least resistance by avoiding the bushes as much as possible and setting his trees in the intervening spaces. A desire for definite information as a basis for improved practice led to the experiments reported here.

EARLY WORK WITH VARIOUS SPECIES

Observations made in other regions on the effect of various shrubs on conifer seedlings may be mentioned briefly. As early as 1912 Kimball and Carter (*6*),[2] working with white pine in Massachusetts, observed that medium or heavy low shade with root competition appeared preferable to no shade and no root competition. Later Hofman (*5*), working in the Cascade Mountain region, concluded that shade was not an important factor in reforestation except when the site is very poor or the shade very dense. Still more recently Show (*10*), working principally with western yellow pine in California, reached these conclusions:

1. Brush cover increases survival, and the benefit of shade is greater on poorer sites, for less drought-resistant species, and for poorer stock.
2. The quality of work done in planting improves as the brush cover decreases.
3. The influence of different species of brush is found to vary greatly. Manzanita is least detrimental to success in planting.
4. Increased shading results in increased height growth.

[1] Received for publication June 13, 1930, issued October, 1930.

[2] Reference is made by number (italic) to Literature Cited, p. 612.

From the early forest planting work in northern Idaho and western Montana it was evident that trees planted in the shelter of stumps and fallen logs usually survived better than those set in more exposed spots. The difference in moisture conditions seemed to be what affected the trees. These casual observations were verified by a special test in the spring of 1923 in which 800 trees were planted and half of them sheltered by shingles driven into the ground close to each plant on the sunny side. Two hundred western white pines (*Pinus monticola*) on a northwest slope and a similar number of western yellow pines (*P. ponderosa*) on a southwest slope were sheltered in this way. Survival of both species of trees was higher when sheltered than when in the open. It seemed natural to expect that the effect of brush on trees, so far as the tops only were concerned, should be similar to the effect of the logs, stumps, and shingles. That the adverse effect of root competition might more than offset the benefit of shelter was suggested by the results of another test made

FIGURE 1.—East slope bearing a scattered stand of *Ceanothus velutinus*. This was the site of the test plantation

that year (1923). Trees planted under bushes of various species and sizes did not do so well as similar ones planted in the open. No conclusions were possible, however, because of the small number of trees and the lack of adequate experimental control. These preliminary tests indicated the need for more intensive experiments.

EXPERIMENTS WITH YELLOW PINE AND CEANOTHUS

INSTALLATION OF TESTS

In the spring of 1926 a mountain slope, considered typical of much of the land in need of planting in the region (fig. 1), was selected for the experiment, near Haugan, Mont. It was a portion of the area burned in 1910 and constituted a uniform easterly slope bearing an evenly scattered stand of *Ceanothus velutinus*. The bushes consisted of numerous stems branching from the root collar, at which point the oldest stems were found to range from 10 to 14 years of age. However, most of the stems were found to be only about half as old

and in their more or less sprawling position rose only from 2 to 4 feet from the ground. In this experiment it was desired to study the effect of brush on western yellow pine, independently of shade from other objects. Accordingly the area selected was one having a minimum number of dead trees either standing or down.

The trees for planting were taken from the general run of 1–2 western yellow pine stock at Savenac nursery after the most poorly developed specimens had been rejected, a number amounting to 13½ per cent of the total. Roots were pruned to a length of 8 inches. Six hundred bushes well distributed over the mountainside were selected, and three trees were planted (April 9–13, 1926) on the slope just below each bush. One tree was placed well under where it received much shade and root competition; one was placed well out where it received no root competition from bushes and very little, if any, shade; and the third tree was set in an intermediate position where it received some shade and doubtful root competition. This intermediate position was under the outer edge of the crown of each bush. All trees were planted by the same man in a uniform manner, using the method standardized for Forest Service planting in the region.

ENVIRONMENTAL FACTORS WORTHY OF STUDY

Apparently inconsistent results are often obtained from experiments with plants simply because of a dearth of information concerning some of the factors involved. However, the multiplicity of these factors and the impossibility of studying them all at any one time or place, necessitates the attempt to measure only a few and to control or eliminate the influence of others. In this experiment only the factors believed to be of most vital importance were studied. Years of experience indicate that of all environmental factors, moisture relations are the most influential on the life of planted trees. This was recognized by Korstian (*7*) working with western yellow pine in Utah. Although light was not studied in this experiment, because of the lack of suitable instruments and the belief that its rôle is subordinate to that of moisture, a study was made of the more readily measurable, and probably more significant, temperature relations.

When soil-moisture determinations can be expressed in terms of moisture available to the crop studied, their significance can be much more readily interpreted than when they are expressed in terms of total moisture. Accordingly, from several points scattered over the site of the test plantation, soil samples were taken to represent the upper 8-inch layer of soil. This earth was then used in the greenhouse for a determination of the wilting coefficient for western yellow pine. The method used was that advocated by Bates and Zon (*3*). The weighted averages employed in this method gave these results: Pan No. 1, 4.1 per cent; pan No. 2, 3.6 per cent; or an average, approximately, of 3.9 per cent, as the wilting coefficient. This figure was then applied to the results of field and laboratory determinations of total moisture, expressed in percentage of oven-dry weight, and shown in Table 1.

The death of plants from drought is due not only to the lack of available soil moisture but almost equally to the loss of moisture through transpiration of the tops. The external factor most directly

affecting transpiration is evaporation, depending as it does on the combined influence of wind, temperature, and humidity, each of which is recognized as an important factor in the survival of plants during periods of drought. Accordingly, a study of evaporation was made involving the locations of the western yellow pines planted under Ceanothus. A typical bush was selected near the center of the plantation and two Bates evaporimeters were placed underneath, two in

FIGURE 2.—View of instruments as installed for a study of evaporation and temperature in relation to Ceanothus brush

the open space on the slope below, and one at the intermediate position under the edge of the crown. (Fig. 2.) A continuous record of evaporation at these three points was thus obtained for the 81 days from June 17 to September 6. Thus the figures given in Table 2 have a sufficient basis to show the average relative rates of evaporation under and away from the bushes during the summer period.

No thorough study was made of atmospheric humidity as an independent factor. Theoretically absolute humidity, because of

transpiration from the foliage and evaporation from the moister soil, would be greater under the bushes than in the open. This condition, and also the lower air temperature in the shade, would cause a still greater contrast in relative humidity under the brush and outside. Such a contrast, if it actually exists over small areas, would naturally be greatest when the sun shines and no wind is blowing. Direct measurements of relative humidity with a cog psychrometer on two calm and sunny days gave the figures shown in Table 3. Undoubtedly average conditions, had they been determined, would show similar though less marked contrasts.

TABLE 1.—*Soil moisture in relation to Ceanothus*

[Moisture in percentage of oven-dry weight of soil]

Date	Position relative to brush	Basis (samples)	Total moisture	Wilting coefficient	Available moisture
1926		*Number*	*Per cent*	*Per cent*	*Per cent*
July 7	Open	7	6.2	3.9	2.3
Do	Intermediate	1	9.1	3.9	5.2
Do	Under	7	9.4	3.9	5.5
Aug. 7	Open	7	3.5	3.9	−.4
Do	Intermediate	1	3.2	3.9	−.7
Do	Under	7	4.5	3.9	.6

TABLE 2.—*Evaporation in relation to Ceanothus*

[Averages per 24-hour day]

Dates	Period	Position relative to bush		
		Under	Intermediate	Open
1926	*Days*	*Grams*	*Grams*	*Grams*
June 17–June 29	11.8	5	7	11
June 29–Aug. 3	35.0	6	10	15
Aug. 3–Sept. 6	34.2	4	6	7
June 17–Sept. 6	81.0	5	8	11

TABLE 3.—*Relative humidity in relation to Ceanothus (read from cog psychrometer)*

Date	Position relative to bush		
	Under	Intermediate	Open
1926	*Per cent*	*Per cent*	*Per cent*
July 2	62	48	47
July 6	44	40	33
Average	53	44	40

That soil temperatures are influential in plant life is generally recognized. The influence of forest cover on soil temperature has been studied recently by Li (*9*). He found that the forest cover near Keene, N. H., reduced the maxima, minima, and means of soil temperatures at all depths through the summer. This forest cover consisted of a canopy of trees and the litter of the forest floor. Brush

cover might reasonably be expected to have a similar, though less marked, effect. Records were obtained by the simultaneous operation of two carefully adjusted soil thermographs with soil bulbs extending from the surface to a depth of 8 inches, one under brush, the other in an adjacent opening. These thermograph traces form the basis for the graph shown in Figure 3. Apparently the brush had a marked effect in lowering soil temperature and reducing its range within the upper 8 inches where the planted roots are. Bates (*2*) emphasizes the importance of high temperatures at the surface of the soil, and Toumey (*11*) found that the surface temperatures varying from 122° to 131° F. killed very young, tender conifer seedlings. Although such high temperatures might not be actually fatal to the 3-year-old trees planted in these tests, it was thought that they might easily affect thrift and early growth. Thermometers observed during the period from June 17 to September 6 indicated the following maximum

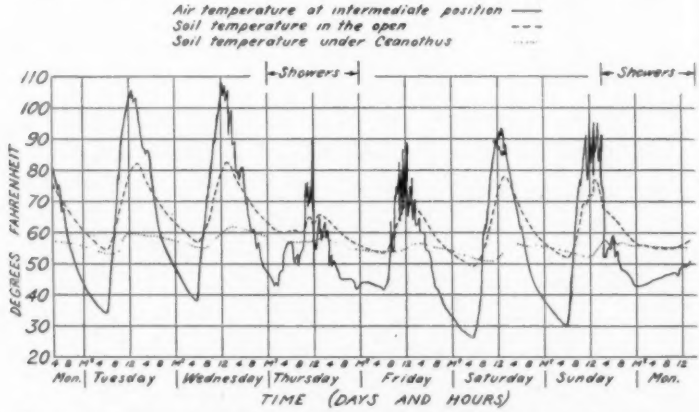

FIGURE 3.—Thermograph tracings showing relations of air temperatures and soil temperatures to a depth of 8 inches on planted area during last week of August, 1926

surface soil temperatures: Under Ceanothus 94°, intermediate position 138°, and open position 145°.

EXAMINATION OF TREES

When the western yellow pines planted in the Ceanothus brush field were examined in August, 1926, the foliage of the current year's growth on shaded trees was strikingly different from that on the unshaded ones. Under Ceanothus the needles on new shoots were longer, thinner, and more delicate in appearance than those grown in the open. The needles within each fascicle on shaded trees were well separated from each other in the normal way, whereas on trees standing in the open the new needles had not separated. These open-grown needles were very noticeably shorter and thicker than those grown in the shade, although not as thick as the long, mature western yellow pine needles from older trees. These differences in external appearance of shade-grown as compared with open-grown needles were so marked that it was thought worth while to look for corresponding differences in internal structure. Korstian (*8*), working

with 3-year-old Douglas fir (*Pseudotsuga taxifolia*) seedlings in seed beds at the Cottonwood nursery in Utah, found that the leaves of shaded plants had a less compact structure, thinner epidermis and cuticle, more spongy tissue, closer lying cells, and less deeply depressed stomata than plants growing in the open sunlight. Laboratory study of the yellow pine needles failed to reveal any such significant differences in cell structure, but it served to illustrate more clearly the relative size of the needles as a whole. Figure 4 shows that the shade-grown needles, although apparently healthy and normal in

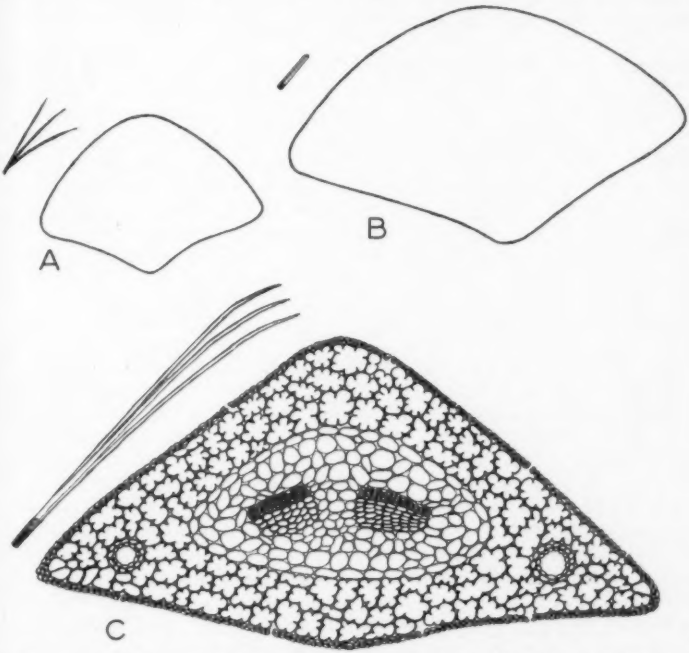

FIGURE 4.—The diagram shows the relative size of needle fascicles (one-half actual size) and cross sections of needles (magnified seventy-five times) from 3-year-old western yellow pine transplants planted (A) under a Ceanothus bush and (B) in the open. The figure also shows (C) fascicles and cross section of a 13-year-old, naturally seeded, open-grown, western yellow pine from the same area. The internal structure of A and B is similar to that shown for C

structure, were much more slender and delicate than the needles from an older open-grown and naturally seeded yellow pine. The needles from the tree planted in the open were intermediate in thickness and doubtless would also have been intermediate in length had it not been for the action of drought. Obviously drought caused a cessation of development in these new needles, leaving them short and closely appressed in the fascicle, as shown in the drawing. This did not happen to the new pine needles under the Ceanothus because of the greater soil moisture and less desiccating atmospheric conditions existing there, as indicated by the above tables.

It was evident that under the bushes evaporation was less, and that, at least during periods of little wind and much sunshine, humidity was higher than in the open. Furthermore, as indicated in Table 1, by the end of the first week in August the moisture available to western yellow pines planted in the open had been completely exhausted, whereas a little available moisture still remained under the bushes. This observation led directly to an examination of each of the 1,800 trees in the plantation, since, theoretically at least, the trees in the open should be found dying in large numbers as a result of the more intense drought in the open spaces. The actual condition of the plantation at that time is shown in Table 4.

TABLE 4.—*Average condition on August 20 of western yellow pines[a] planted April 9–13, 1926, among Ceanothus bushes on an east slope in western Montana*

Condition	Open position	Intermediate	Under Ceanothus
	Per cent	*Per cent*	*Per cent*
Thrifty	40	57	80
Unthrifty	13	11	9
Alive	53	68	89
Dead	47	32	11

[a] Basis, 600 trees in each of the three positions.

This table indicates clearly that the trees planted closely under the brush survived best during the dry season following spring planting. It seemed that the problem was already more than half solved because the first dry season is always the most critical time in the life of the planted trees. The possibly keener competition in the future between the more deeply penetrating roots of the trees and shrubs is not especially to be feared, because the shock associated with planting will have been outgrown and the tops of the bushes will still provide beneficial shelter from extreme atmospheric conditions. So far as the attainment of high survival is concerned, it seems safe to recommend that yellow pines be planted as close to Ceanothus bushes as is practicable without appreciably lowering the quality of planting.

However, this early high survival under brush will be useless if the bushes ultimately "smother out" the trees. It is not always true that those environmental conditions which favor plant life in general favor both survival and growth. Sometimes the same conditions that favor survival retard growth and vice versa. Such an observation was made on western white pine in an earlier study (*12*), in which trees planted on a steep northwest slope survived best of all the lots tested but grew least rapidly, while the trees on the severe west slope survived least well, but grew most rapidly during the first three years following planting. Similarly in the present study it may be found that the conditions that favored high survival under the bushes may be such as to retard growth of the trees. However, it does not seem likely that Ceanothus can permanently suppress these yellow pines when one considers the prevalence of brush fields following destructive fires and the widely accepted idea that all stands of timber represent a more advanced stage in plant succession in timber regions than do the shrub types. Proof of the natural

dominance of the trees or brush in this experiment can be finally obtained only by observation of the trees year after year until they have either died or grown out above the bushes. In the meantime it seemed desirable to gather empirically some evidence of the probable result of this association of brush and trees. About a week was spent in scouting through various brush areas to observe whether or not naturally seeded trees were successful when they happened to start life close to various bushes, especially Ceanothus. A special hunt was made for trees that had emerged above the brush or died in the attempt. In several cases, where yellow pines were found emerging above dense brush, the trees were found to stand but a few inches from the root collars of older bushes, a condition indicating that the bushes had a start in the race with trees that grew well within the soil areas the bushes utilized. Although many instances were found of trees successfully emerging after apparently keen competition, it seems significant that only one failure was discovered. No statistical summary of these observation can be presented, but Figures 5 to 8 illustrate special cases which have a bearing on the subject.

Such observations appear to indicate that brushes hinder growth of tree seedlings only temporarily, if at all, and that such hindrance will increase the rotation period in timber growing by a negligible amount.

Ceanothus is one of the few nonleguminous plants that is suspected of harboring bacteria that add nitrogen to the soil in available form. Arzberger (*1*) and Bottomley (*4*) report finding root nodules on this genus and the writer has observed them on the roots of the local species. That nitrogen in a form available for the use of plants is lost from the soil as a result of forest fires is often overlooked. Yet available nitrogen is one of the elements of soil fertility that most profoundly affects the growth of trees. If stands of Ceanothus fix nitrogen in the soil in appreciable amounts on burned areas, they may increase the rate of tree growth for many years after their protection against loss of trees from drought is no longer needed. Except in fully and evenly stocked young stands of pine, Ceanothus bushes frequently live among the trees during their sapling and pole stages or longer, and as long as the shrubs do so persist they may be stimulating the growth of the timber, and thus Ceanothus may be an asset even beyond its early beneficial effect in forest regeneration.

SUMMARY

During dry summer weather in western Montana it was found that under Ceanothus brush atmospheric evaporation was less, relative humidity greater, soil temperature lower, and soil moisture greater in amount than in adjacent open spaces. As a result of such conditions it was also found that survival of western yellow pines during their first dry season following field planting was much higher under the bushes than in the open. Although future records of growth are needed to show definitely whether or not the trees under the brush can successfully emerge, observations of natural reproduction indicate that brush can not permanently suppress tree growth.

FIGURE 5.—The seedling in front of the white paper is 6 years old, 14 inches high, and stands 7 inches from the root collar of an 11-year-old bush. Although the dense Ceanothus brush is 2 to 3 feet high and completely covers the seedling, the tree grew 3¼ inches during its last year (1926). Its thrifty condition indicates that it has a good chance to emerge eventually

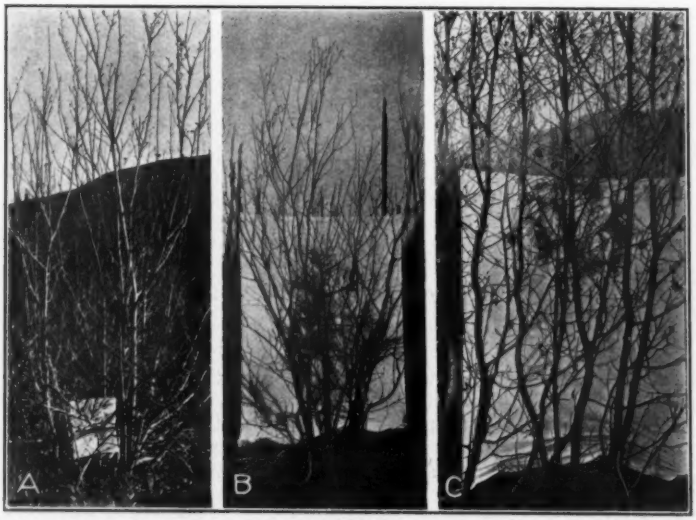

FIGURE 6.—A, The western yellow pine seedling, in front of the white paper, is 5 years old and 14 inches tall. The service-berry bush is 8 years old and 11 feet 5 inches tall. Both are in thrifty condition; B, this yellow pine is 8 years old and 4 feet 7 inches tall, and the willow bush is 11 years old and 8 feet 7 inches tall. In spite of the fact that the pine stands in actual contact with the root collar of an older and thrifty bush, the tree grew about 8 inches during each of the last 4 years; C, this western pine is 10 years old, 5 feet 9 inches tall. It stands in contact with the root collar of a 10-year-old alder bush that is 14 feet 4 inches tall. Although the tree is slender, as a result of the dense shade, it is healthy and growing

FIGURE 7.—The western yellow pine in the center sprang from seed and is now emerging above dense Ceanothus brush. The 11-year-old tree stands 13 inches from the root collar of a 13-year-old bush

FIGURE 8.—The center pine in this picture sprang from seed 13 years ago. It is now well above the 14-year-old Ceanothus bushes that crowd it from all sides. The root collar of the nearest bush is 7 inches from the base of the tree

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THE NATURE OF SMUT RESISTANCE IN CERTAIN SELFED LINES OF CORN AS INDICATED BY FILTRATION STUDIES [1]

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INTRODUCTION

One of the prime considerations in the selection and breeding of crop plants is the development of strains that are resistant to or immune from disease. In general, however, relatively little is known of the fundamental nature of disease resistance in plants. Such is the case in regard to resistance of corn (*Zea mays*) to smut. The corn breeder has produced many lines and crosses resistant to smut and has discovered many facts in regard to the inheritance of resistance and susceptibility in corn,[3] yet the fundamental nature of its resistance is not known.[4] This paper presents the results of experiments to determine whether or not the juices of the various parts of certain resistant strains of corn are factors in resistance and whether or not they contain a susbstance inimical to the growth of the smut fungus.

MATERIALS AND METHODS

In order to provide plant material of definite genetic constitution and of known smut reaction under field conditions, selfed lines of corn and their crosses were used.

The smut used to furnish inoculum for the filtrates was selected from a group of collections made in various parts of the United States during the summer of 1927 and was cultured from gall tissue. The collection number of each smut and the locality in which it was collected are as follows: No. 3–2, Clemson College, S. C.; No. 34–2, Mesilla Park, N. Mex.; No. 50–1, Davis County Experiment Farm, Utah; No. 60–2, Manhattan, Kans.; No. 74–2, University Farm. St. Paul, Minn.; No. 92–2, Provincetown, Mass.

The corn plants from which the juices were extracted were grown in the greenhouse during the autumn and winter of 1927–28. The experiments were repeated on plants from the same lots of seed grown in the field at the Arlington Experiment Farm, Rosslyn, Va., during the summer of 1928. The plants used were cut and separated into

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[2] The writer wishes to express his indebtedness and appreciation to the following persons for their cooperation in supplying seed for use in the experiments herein reported: C. H. Kyle, F. D. Richey, J. M. Hammerly, J. H. Martin, H. N. Vinall, A. M. Brunson, J. R. Holbert, M. T. Jenkins, J. F. Trost, and G. M. Smith, of the Bureau of Plant Industry, U. S. Department of Agriculture; H. K. Hayes and F. R. Immer, of the University of Minnesota; D. F. Jones, of the Connecticut Agricultural Experiment Station; R. J. Garber, of the University of West Virginia; L. E. Melchers and C. H. Ficke, of the Kansas State Agricultural College; A. H. Eddins, of the Iowa State College of Agriculture and Mechanic Arts; and W. T. Conway, of the New Mexico College of Agriculture and Mechanic Arts. The writer is indebted to Mr. Kyle also for many helpful suggestions and criticisms.

[3] IMMER, F. R. THE INHERITANCE OF REACTION TO USTILAGO ZEAE IN MAIZE. Minn. Agr. Expt. Sta. Tech. Bul. 51, 62 p., illus. 1927.

[4] Recently Kyle has shown that in certain strains of corn the tightly inclosing husks protect the ears from smut. KYLE, C. H. RELATION OF HUSK COVERING TO SMUT OF CORN EARS. U. S. Dept. Agr. Tech. Bul. 120, 8 p., illus. 1929.

leaf, stalk, and husk parts. These were ground separately through a mill equipped with medium-grade plates. The ground material thus obtained was weighed and the juice extracted for one and one-half minutes by means of a hydraulic press at a pressure of 4,000 pounds. The extracted juice was measured and filtered immediately. The filtration apparatus used in this work has been described in detail in a previous paper.[5]

The apparatus in operation is illustrated in Figure 1.

When sufficient filtrate had been collected in the 250 c. c. Erlenmeyer flasks, the vacuum was released very slowly. The flasks were then disconnected so that each carried the rubber stopper, the bent glass tube filled with sterile cotton, and the short rubber-tube connection (with the screw clamp firmly set) attached to the side arm. The liquid in each flask was thus protected against contamination. The filtrate was removed from the flask by pouring it out through the side arm, after the rubber-tube connection had been removed and the tip of the side arm gently heated.

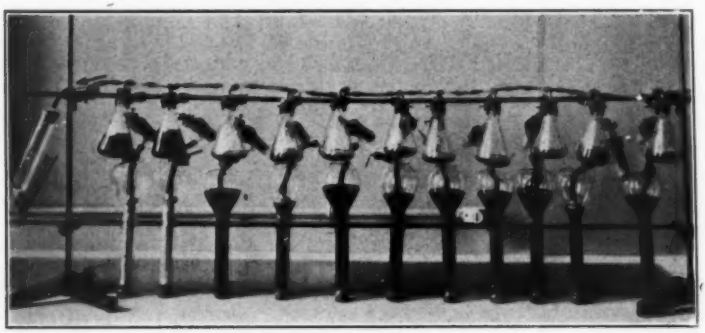

FIGURE 1.—Battery of filtration units in operation. Most of the weight of each unit is supported by the burette clamps around the necks of the Erlenmeyer flasks containing the filtrate. The vacuum is connected by means of glass T tubes and thick-walled rubber tubes of suitable length. All connections not subject to sterilization are shellacked to guard against possible leaks

After all the flasks of a filtration battery had been disconnected, they were taken into a previously steamed transfer room. Here 5 c. c. portions of the sterile filtrate were measured into sterile test tubes and inoculated with one drop of a smut culture that had grown six days in a nutrient solution.

When the work was first started the filtrates were measured and inoculated by means of sterile pipettes, but this method was extremely slow and resulted in a large number of contaminations. A rapid and satisfactory method involving the apparatus shown in Figures 2 and 3 was worked out. The following technic in using the apparatus was found successful. It was first assembled and sterilized in an autoclave at 15 pounds pressure for 30 minutes. Then the test tube over the end of the burette was removed and the sterile filtrate was poured into the burette from the filter flask through the side arm of the flask after the rubber connection had been removed and the tip of the side arm had been gently heated. The cotton plug in the mouth

[5] RANKER, E. R. APPARATUS AND METHODS FOR OBTAINING STERILE FILTRATES OF BIOLOGICAL FLUIDS. Phytopathology 20: 569-573. 1930.

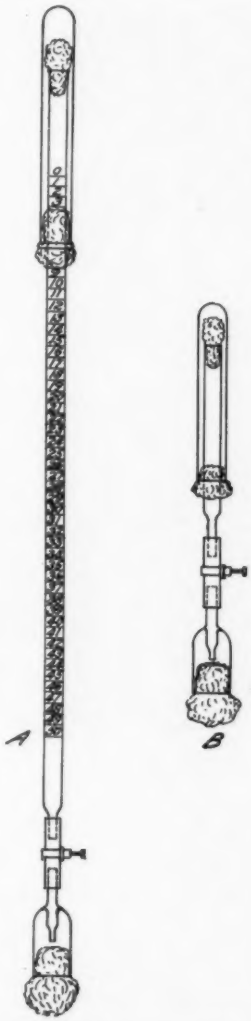

FIGURE 2.—Apparatus used in measuring (A) and inoculating (B) sterile plant filtrates: A, Burette for holding a sterile filtrate of extracted juice from corn; B, inoculum tube for holding the liquid medium containing conidia of *Ustilago zeae* in pure culture. The outlet tips with protecting shields are shown just above the lowermost cotton plugs in A and B

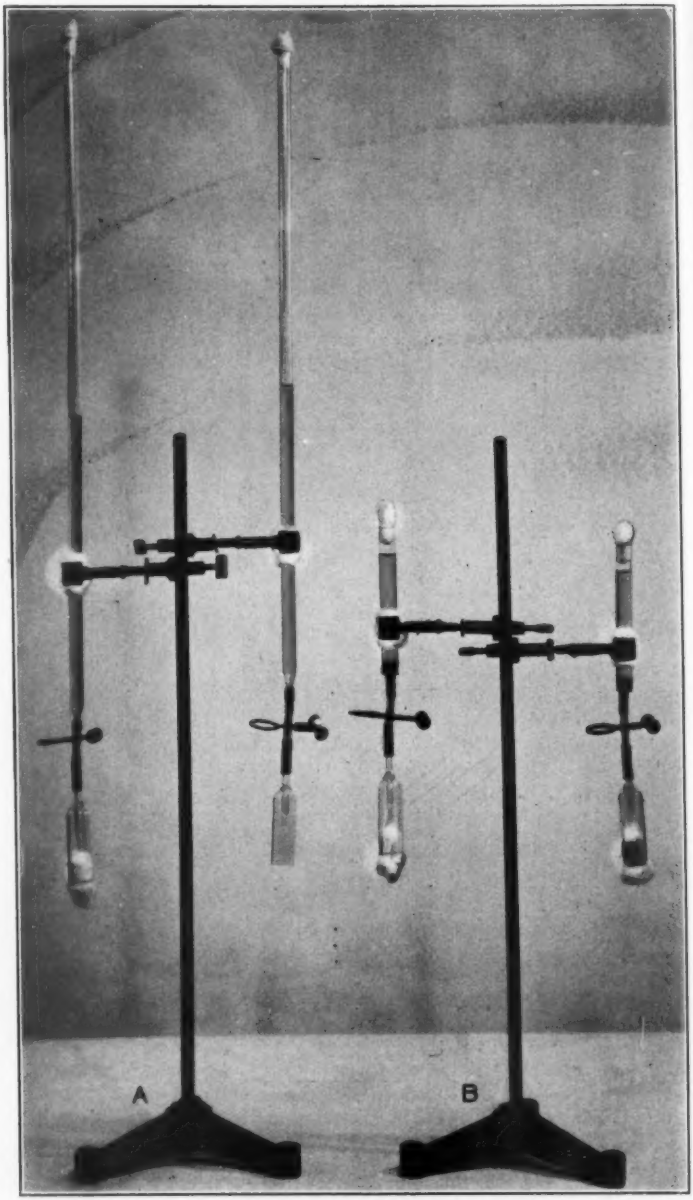

FIGURE 3.—Apparatus shown in Figure 2 set up for operation: A, Burettes containing filtrates; B, tubes containing inoculum. The lower cotton plug has been removed from one of the burettes to show the manner of exposing the outlet tip as described in the text

of the burette was reinserted after the burette was filled. The inoculation device (fig. 2, B) was filled with inoculum in a similar manner. The cotton plug protecting the outlet tip of the inoculation tube was removed and the screw clamp so adjusted that the inoculum would come out at the desired frequency a drop at a time. The sterile test tubes were filled from the burettes with a measured quantity of the sterile filtrate. After each tube was filled it was immediately passed under the inoculation tube to receive one drop of the proper inoculum and then replugged. The cotton plugs protecting the burette tips were not removed until just before the sterile tubes were filled. The glass shields around the outlet tips were large enough to admit the mouth of the test tube readily, but small enough to make it impossible for the test tube to come in contact with the outlet tip. All of the special glass apparatus shown was made from Pyrex glass.

Triplicate cultures of each smut were prepared as above described, and the cultures were allowed to grow at room temperature for a period of one month or six weeks, the period being the same for comparable lots. At the end of the incubation period the amount of growth of the smut was measured in terms of the quantity of fungus obtained by centrifuging at 1,800 revolutions per minute for three minutes. Small conical centrifuge tubes, having standardized calibrations reading to one-tenth of a cubic centimeter, were used.

RESULTS

USING FILTRATES FROM WHOLE CORN PLANTS

Preliminary experiments were undertaken in which filtrates were used that had been obtained by grinding the whole plant excluding the roots. Material representing most of the available smut-resistant and smut-susceptible selfed lines and crosses was tested. Some differences were observed in the quantity of smut developed in the various filtrates, but these were not significant. There was abundant growth of all the smuts in all the filtrates tested. In no case did any of the filtrates show an appreciable inhibiting effect on the growth of *Ustilago zeae*. This was true regardless of whether the filtrate was obtained from the juice of a resistant or a susceptible selfed line or cross.

USING FILTRATES FROM VARIOUS PARTS OF CORN PLANTS

A second group of experiments was made in which filtrates obtained from various parts of the plant were used. The plants were grown in the greenhouse at the Arlington Experiment Farm during the early autumn of 1927. They were allowed to develop until the silks appeared. At this stage, or during the week following, the plants were harvested and separated into husk, leaf, and stalk parts. The filtrate juices of these parts were used in tests as above described. The results from representative plants are given in Table 1.

TABLE 1.—*Growth of Ustilago zeae in sterile unheated filtrates of expressed juice from husks, leaves, and stalks of plants of selfed lines and crosses of smut-resistant and smut-susceptible corn grown in the greenhouse at Arlington Experiment Farm, Rosslyn, Va., during autumn of 1927*

Host material	Degree of resistance [a]	Part of plant used	Growth of [b] smut culture No.—					
			3–2	34–2	50–1	60–2	74–2	92–2
Silver King No. 67	High	Husk	0.03	0.07	0.03	0.02	0.05	0.07
		Leaf	.15	.20	.15	.10	.10	.15
		Stalk	.70	.45	.55	.50	.60	.40
Silver King No. 72	do	Husk	.10	.10	.10	.10	.10	.15
		Leaf	.25	.30	.25	.20	.25	.30
		Stalk	.70	.70	.60	1.00	.70	.70
Rustler No. 35	do	Husk	.05	.05	.06	.05	.07	.20
		Leaf	.10	.11	.10	.10	.12	.20
		Stalk	.60	.70	.60	.70	.70	.65
Salmon Silk No. 14	Medium	Husk	.40	.30	.45	.30	.40	.35
		Leaf	.15	.16	.15	.20	.15	.20
		Stalk	.90	.90	1.10	1.05	1.05	.80
Kansas Sunflower 3389(3)×3400(7)	Medium to high	Husk	.76	.80	.70	.70	.70	.70
		Leaf	.60	.60	.50	.45	.55	.65
		Stalk	1.05	1.30	1.25	.90	.55	.60
C. I. 240–F–577e×C. I. 240–F–577c, 1927	High	Husk	.45	.50	.50	.50	.40	.30
		Leaf	.45	.30	.45	.50	.40	.40
		Stalk	.60	.80	.70	.70	.75	.60
C. I. 207–F–90×C. I. 218–F–69, 1927	Low	Husk	.92	.75	----	----	----	----
		Leaf	.63	.57	----	----	----	----
		Stalk	.45	.50	----	----	----	----
Brown Aleurone No. 13	do	Husk	.30	.37	----	----	----	----
		Leaf	.40	.60	----	----	----	----
		Stalk	.70	.90	----	----	----	----

[a] Information furnished by the corn breeders who supplied the seed from which the host materials were grown.

[b] Growth is expressed as cubic centimeters of fungus thrown down after centrifugation at 1,800 r. p. m. for 3 minutes. Details and reasons for using this method are given in a previous paper: RANKER, E. R. SYNTHETIC NUTRIENT SOLUTIONS FOR CULTURING USTILAGO ZEAE. Jour. Agr. Research 41: 435–443, illus. 1930.

The data of Table 1 show results entirely different from those obtained from the mixed juices of whole plants. There are striking differences in the growth of *Ustilago zeae* in the sterile filtrates of juice from husks, leaves, and stalks. The filtrates of the husk-tissue juice of Silver King No. 67, Silver King No. 72, and Rustler No. 35, varieties highly resistant under field conditions, show a decided inhibiting action on the growth of *U. zeae*. The juice from the leaves of Salmon Silk No. 14, a medium-resistant variety, seems to possess the greatest relative inhibiting action. Juices from two resistant crosses, Kansas Sunflower 3389(3)×3400(7) and C. I. 240–F–577e×C. I. 240–F–577c, seem to possess no marked inhibiting power. Data from two smut-susceptible lines included in Table 1 illustrate a reaction found for all susceptible lines tested, namely, that the filtrate from no plant portion showed any marked inhibiting effect on the growth of *U. zeae*.

It is worthy of note that filtrates inhibiting the growth of *U. zeae* gave the same result with all the smut collections tested, regardless of the locality from which they came, and regardless of the fact that they undoubtedly represented different physiologic forms, two collections (Nos. 60–2 and 74–2) being especially virulent.

DISCUSSION AND CONCLUSIONS

The foregoing results indicate a type of resistance in which the host contains some soluble substance in the tissue juice that inhibits the growth of *Ustilago zeae*. This inhibiting substance was not

found in the juice of any part of any of the susceptible lines tested nor in some of the resistant lines.

In some of the lines the substance was most inhibiting in the husk juice, as in Silver King No. 67. In other lines the leaf juice was relatively most inhibiting to the fungus growth, as in Salmon Silk No. 14. The fact that some smut-resistant lines of corn fail to give positive results from the filtrate studies indicates the existence of other types of resistance. Lines of corn that possess resistance due to some inhibiting substance present in their juices conceivably may be resistant because of other factors also.

One interesting feature of the results obtained in this study was the constancy of the inhibitory effect with all the smut cultures tested, regardless of difference in physiologic forms and virulence. As noted above, two of the smut cultures were especially virulent on most of the pure lines and crosses. This uniform result is significant in view of complications presumably introduced by different physiologic forms of smut.

There is need of more information and study. The data at hand, however, are suggestive of a promising objective in corn breeding. The methods here reported might well serve to aid in selecting selfed lines and crosses possessing resistance to the smut organism.

18496—30——4

INFLUENCE OF HULLING THE CARYOPSIS ON COVERED-SMUT INFECTION AND RELATED PHENOMENA IN OATS[1]

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INTRODUCTION[3]

In the course of breeding experiments for the development of economic strains of oats resistant to *Ustilago levis* (K. and S.) Magn., the writers have recorded data on the influence of removing the hull from the caryopsis on (1) covered-smut infection, (2) seedling emergence, (3) number of plants reaching maturity, and (4) inheritance of resistance to covered smut.

Investigators are not in accord regarding the value of hulling before artificially inoculating seed with covered-smut spores for the determination of relative susceptibility and resistance in oats. In the present investigations, in which thousands of plants were grown in comparable experiments from inoculated unhulled and hulled seed, the number of smutted plants was greatly increased by hulling. It is generally held that the spores of the covered-smut fungus are brought in contact with the seed in the threshing of healthy and smutted panicles, and that the smut spores overwinter on the exterior of the hulls. In the process of threshing, a small percentage of the seed usually is hulled. In view of this fact, it is desirable in breeding oats to select hybrids that are resistant to or immune from covered smut even when the inoculum is applied to the naked kernel or caryopsis.

In connection with this study some data were obtained on the percentage of seedling emergence and on the number of plants maturing from unhulled and hulled seed. The influence of hulling on the number of smutted and smut-free segregates in hybrid populations also was noted.

These studies were made at Ames, Iowa; Dickinson, N. Dak.; Moro, Oreg.; Aberdeen, Idaho; and Moccasin, Mont., in cooperation with the respective State agricultural experiment stations. At Ames conditions are typical of the so-called Corn Belt and are entirely distinct from the dry, semiarid conditions prevailing at Dickinson, Moccasin, and Moro. At Aberdeen still another set of conditions prevails—an arid climate, with the water for crop production supplied by irrigation. The value of the data is increased by the wide variation in climatic and other environmental conditions under which they were obtained.

[1] Received for publication July 3, 1930; issued October, 1930. The investigations here reported were conducted by the Office of Cereal Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture, in cooperation with the Iowa, North Dakota, Montana, Idaho, and Oregon Agricultural Experiment Stations.

[2] The writers are indebted to L. C. Burnett, Chief in Cereal Breeding, Iowa Agricultural Experiment Station, for assistance in conducting the experiments at Ames.

[3] In several previous publications of the Office of Cereal Crops and Diseases the term "dehulled" was used to designate the removal of the glumes (lemma and palea) from the caryopsis or groat. In this paper "unhulled" designates the kernel with the glumes attached, and "hulled" the caryopsis from which the lemma and palea have been removed.

REVIEW OF LITERATURE

As early as 1887 Jensen (*11*)[4] observed that smut infection in oats was increased by removing the hull before artificially inoculating the seed. Johnston (*12*) reported that the removal of the glumes (hulls) from oats caused a large increase in the percentage of infection by loose and covered smuts. The increase in infection was largest in susceptible and moderately susceptible varieties and much smaller in resistant varieties. A study was made of the smut reaction of plants grown from hulled seed of the Burt and Kanota varieties, resistant to the inoculum used. The data indicated that Burt derived part of its resistance to smut from the mechanical protection afforded by the glumes. The resistance of Kanota was not primarily due to glume protection. Johnston concludes that some varieties of oats escape infection through the protection of their glumes, while others are relatively free from smut because of inherent resistance.

One hundred per cent infection, however, is not obtained with hulled seed. Gage (*6*) suggests that some of the covered-smut spores are disseminated in time to enter late-blooming flowers while the glumes are open and that these spores are a more effective source of inoculum than those that are brought in contact with the outside of the hulls in threshing.

Gaines, as reported by Schafer (*19, p. 31*), and Stanton, Stephens, and Gaines (*21*) present data which indicate that a much higher infection with *Ustilago levis* was obtained by removing the oat hulls.

Garber, Giddings, and Hoover (*9*) tried various methods, including hulling seed before treating with smut, in producing an artificial epidemic, but made no direct statement relative to the effect of hulling.

Sampson (*18*) notes that removing the husk (hull) increased infection of the Potato variety of oats as much as 33.8 per cent, and that of *Avena strigosa pilosa* with *Ustilago avenae* and *U. levis* 42.9 per cent. She also notes that susceptible varieties show considerably increased infection after hulling but that resistant varieties are not affected.

Bayles and Coffman (*2*) present data which show that a much higher infection of covered smut is obtained by hulling the oat caryopsis.

Tisdale (*22*) and Tisdale and Tapke (*23*) have demonstrated that infection of barley with loose and covered smuts can be increased by removing the glumes before applying smut spores to the seed.

Barney (*1*), Reed (*13, 14*), Reed, Griffiths, and Briggs (*16*), Reed and Faris (*15*), Reed and Stanton (*17*), Wakabayashi (*24*), Gaines (*7, 8*), and Hayes, et al. (*10*) all have reported experiments on the relative susceptibility or on the inheritance of resistance to smut of oats when the hull was not removed before inoculation.

MATERIALS AND METHODS

Ten varieties, 200 pure-line selections from the unnamed oat C. I.[5] No. 357, and hundreds of selections from seven different crosses, were used in the studies reported in this paper. The history of this plant material is presented in the following paragraphs. Methods of inoculating seed and of recording data also are outlined briefly.

[4] Reference is made by number (italic) to Literature Cited, p. 632.
[5] "C. I." indicates accession number of the Office of Cereal Crops and Diseases.

PARENT VARIETIES

The varieties used as parents of hybrids were Markton, Aurora, Idamine, Iogren, Scottish Chief, Silvermine, Swedish Select, and Victory. All of these varieties belong to the common oat group, *Avena sativa*.

MARKTON.—The history, description, and probable value to oat breeding of the smut-immune variety Markton (C. I. No. 2053) have been recorded by Stanton, Stephens, and Gaines (*21*). It is an early to midseason variety with large panicles and rather long, slender to midplump, yellow kernels. So far as known, Markton has been uniformly immune from the smuts of oats in all experiments conducted in the United States. Markton is of commercial importance in Oregon, Washington, Idaho, and adjacent Montana.

AURORA.—This variety (C. I. No. 831) has not been described previously. It originated at the Arlington Experiment Farm, Rosslyn, Va., as a selection from Red Rustproof. The original selection was made by C. W. Warburton in 1909. Aurora has been grown experimentally from both fall and spring seeding. It is an early, short to midtall variety with a very short, plump, yellow awnless kernel. The variety is not economically important. It is susceptible to both loose and covered smut.

IDAMINE.—Stanton, Griffee, and Etheridge (*20*) have described Idamine (C. I. No. 1834). It is a midseason variety with very white kernels, and is moderately susceptible to the smuts of oats. Idamine is of some economic importance under irrigation in southern Idaho.

IOGREN.—This variety (C. I. No. 2024) has been described by Burnett, Stanton, and Warburton (*3*) and by Stanton, Griffee, and Etheridge (*20*). It is a midseason variety with yellow kernels and is of considerable economic importance in northern Iowa. Iogren is highly susceptible to the smuts of oats.

SCOTTISH CHIEF.—This variety (C. I. No. 1699) apparently was introduced from Scotland about 30 years ago. Scottish Chief is described by Etheridge (*5*) as a midseason white oat. Scottish Chief is of minor importance as an agricultural variety in the United States.

SILVERMINE.—Silvermine (C. I. No. 1013) apparently was first introduced to the seed trade in 1897 by a commercial seed company of La Crosse, Wis. It is a standard midseason white variety and is generally grown throughout the northern part of the United States. It is described by Etheridge (*5*).

SWEDISH SELECT.—This variety (C. I. No. 134) was introduced into this country by the United States Department of Agriculture in 1899 (*4*). Swedish Select is a midseason white oat of considerable commercial importance in the United States. It has been described by Reed and Stanton (*17*) and by Etheridge (*5*).

VICTORY.—This variety (C. I. No. 560) was originated about 1904 at the Plant Breeding Station, Svalöf, Sweden. It is a pure line of the old Probsteier variety. It was first introduced into the United States in 1908 by the United States Department of Agriculture. Victory is a midseason white oat and differs mainly from Swedish Select in having fewer awns and a slightly less plump kernel. Owing to its high yield and excellent kernel characters Victory has become a leading variety in the irrigated sections, as well as in the more northern oat sections of the United States.

Reed, Griffiths, and Briggs (*16*) presented data showing Aurora, Scottish Chief, Silvermine, and Victory as highly susceptible to the smuts of oats. They indicated Swedish Select as moderately susceptible. These results agree fairly well with those presented in this paper. However, in the writers' experiments Scottish Chief seemed to possess more resistance than any of the other varieties crossed with Markton. Swedish Select, on the other hand, was more than moderately susceptible in the writers' tests.

In addition to Markton the Early Champion and Sixty-Day varieties have been used for the study of the influence of hulling on emergence. The origin of Early Champion (C. I. No. 1623) has not been determined. Etheridge (*5*) described it as an early, white-kerneled variety. Early Champion was grown extensively in the Corn Belt a quarter of a century ago, but to-day it is of little commercial

importance. It is highly susceptible to the smuts of oats, as observed many years ago and confirmed by Reed, Griffiths, and Briggs (*16*).

The Kherson or Sixty-Day variety has been fully described by Warburton and Stanton (*25*). Most of the strains of this oat have been moderately resistant or moderately susceptible to the smuts of oats. The particular strain of Sixty-Day (C. I. No. 165–1) used in the experiment herein reported is highly susceptible to the smuts of oats, as shown by Bayles and Coffman (*2*).

SELECTIONS STUDIED

The smut resistance of the unnamed parent variety C. I. No. 357, from which the smut-immune variety Markton was selected, has been a matter of some interest. This unselected introduction had been discarded on most agricultural experiment stations several years before the discovery of the value of Markton. Through John H. Martin [6] remnant seed was located at the Belle Fourche Field Station, Newell, S. Dak. An increase plot from this seed was grown at Aberdeen, Idaho, in 1924, from which the selections used in the studies reported herein were made.

CROSSES STUDIED

Studies were made on relative smut infection in progenies grown from unhulled and hulled seed of the following crosses involving the parent varieties discussed previously:

Markton×Scottish Chief
Markton×Idamine
Markton×Victory
Markton×Swedish Select
Aurora×Markton
Iogren×Markton
Silvermine×Markton

The first five of these crosses were made by G. A. Wiebe at the Aberdeen Substation, Aberdeen, Idaho, in 1923. The last two were made at the same station by T. R. Stanton in 1924. The F_1 plants of the first five crosses were grown in the greenhouse at the Arlington Experiment Farm, Rosslyn, Va., in the winter of 1923–24. The F_2 populations were grown at the Aberdeen Substation in 1924. The F_1 plants of the last two crosses were grown at the Arlington Experiment Farm in the winter of 1924–25, and the F_2 populations at the Aberdeen Substation in 1925.

SEED INOCULATION

The inoculum used in these experiments came from a collection made at the Aberdeen Substation, Aberdeen, Idaho, in 1924. This collection was predominantly *Ustilago levis* with a trace of *U. avenae*. Fully 99 per cent of the spores were entirely smooth (*U. levis*), the remaining 1 per cent being minutely echinulate (*U. avenae*).

One method of applying the inoculum was followed uniformly throughout these experiments. The seed for each row was placed in its respective seed envelope and a liberal quantity of smut spores was added. The envelope was then shaken vigorously to cover the seed thoroughly with the spores.

In 1925 one half of the seed of each selection or variety included in the various smut experiments was hulled, while the other half was not hulled before inoculation. This method also was largely followed

[6] Of the Office of Cereal Crops and Diseases.

in 1926. Because of the marked increase in the number of smutted plants obtained from hulled seed in 1925 and 1926, all seed sown in these experiments since the latter year was hulled before being artificially inoculated with smut spores. For comparing the relative infection in progenies grown from unhulled and hulled seed data are available only for 1925 and 1926. The hulls were removed in the laboratory with small dissecting tweezers or a penknife blade.

RECORDING OF DATA

The percentage of smut infection was calculated on the basis of the plant as the unit. Any plant showing the merest trace of smut was considered infected.

EXPERIMENTAL DATA

INFLUENCE OF HULLING ON INFECTION IN VARIETIES AND HYBRIDS

Table 1 gives the data on the smut infection of the crop grown from unhulled and hulled seed for the different varieties and their hybrids.

A decidedly higher percentage of smutted plants was obtained in the progenies grown from hulled seed. At Aberdeen in 1925 the average percentage of infection for the three parent varieties grown from hulled seed was 72.6 per cent and from unhulled seed 44.0. In the hybrid progenies the percentages obtained from hulled and unhulled seed were 11.4 and 4.7, respectively. The results at Aberdeen in 1926 varied slightly from those of 1925, but were similar, and for the two years were consistent and conclusive.

At Ames, Iowa, however, a less satisfactory infection was obtained, owing to unfavorable weather conditions at seeding and thereafter. The four parent varieties in 1926 showed an average infection from hulled seed of 50.2 per cent as compared with 16.2 per cent for unhulled seed. In the selections from crosses the percentages were 9.2 and 0.5, respectively.

At Dickinson, N. Dak., in 1925, Swedish Select showed an average infection of 80.6 per cent in the plants grown from hulled seed, while 75.6 per cent of those grown from seed not hulled were infected. The relative difference in the parent varieties between unhulled and hulled seed for some reason is much less at Dickinson than at Aberdeen or Ames. The selections from the Markton × Swedish Select cross at Dickinson, however, showed an average infection of 14.8 per cent from hulled seed as compared with 3.6 per cent from unhulled seed.

The Scottish Chief variety at Moro, Oreg., in 1925 produced 24.6 per cent smutted plants from hulled seed and 11.1 per cent from unhulled seed. A similar spread in infection for the two classes of seed was obtained in the selections of the Markton × Scottish Chief cross.

In all, 2,848 parental and 14,670 hybrid plants were studied. Hulling the seed of the parent varieties increased infection in the resulting crop from 35.2 per cent in plants grown from unhulled seed to 63.8 per cent from hulled seed, and in the hybrids from 3.8 per cent in plants grown from unhulled seed to 12.8 per cent from hulled seed. Where smut-resistant strains of oats are a primary object in the breeding program, greater progress may be made by hulling the seed.

TABLE 1.—*Smut infection* [a] *of oat varieties and hybrid populations grown from unhulled and hulled seed at one or more of four experiment stations in 1925 and 1926*

Station and year	Parent or hybrid	Plants grown from—											
		Hulled seed						Unhulled seed					
		Total		Infected				Total		Infected			
		Number	*Number*	*Number*	*Number*	*Per cent*	*Per cent*	*Number*	*Number*	*Number*	*Number*	*Per cent*	*Per cent*
Aberdeen, Idaho: 1925	Idamine	158		121		76.6		202		62		30.7	
	F_3 Markton×Idamine		161		33		20.5		157		9		5.7
	Aurora	202		110		54.5		210		119		56.7	
	F_3 Markton×Aurora		2,647		242		9.1		2,659		100		3.8
	Victory	151		140		92.7		209		92		44.0	
	F_3 Markton×Victory		622		117		18.8		618		52		8.4
Total or average	Parents	511		371		72.6		621		273		44.0	
	Hybrids		3,430		392		11.4		3,434		161		4.7
1926	Idamine	170		104		61.2		189		49		25.9	
	F_4 Markton×Idamine		87		12		13.8		79		5		6.3
	Victory	177		136		76.8		218		86		39.4	
	F_4 Markton×Victory		75		16		21.3		69		7		10.1
Total or average	Parents	347		240		69.2		407		135		33.2	
	Hybrids		162		28		17.3		148		12		8.1
Ames, Iowa, 1926	Idamine	110		68		61.8		146		32		21.9	
	F_4 Markton× Idamine		12		6		50.0		580		0		0
	Victory	72		29		40.3		77		7		9.1	
	F_4 Markton×Victory [b]		592		0		0		802		0		0
	Iogren	41		16		39.0		43		2		4.7	
	F_3 Markton×Iogren		300		70		23.3		360		6		1.7
	Silvermine	44		21		47.7		49		10		20.4	
	F_3 Markton×Silvermine		56		12		21.4		67		3		4.5
Total or average	Parents	267		134		50.2		315		51		16.2	
	Hybrids		960		88		9.2		1,809		9		.5
Dickinson, N. Dak., 1925	Swedish Select	103		83		80.6		82		62		75.6	
	F_3 Markton×Swedish Select		1,916		284		14.8		1,833		66		3.6
Moro, Oreg., 1925	Scottish Chief	114		28		24.6		81		9		11.1	
	F_3 Markton×Scottish Chief		585		114		19.5		393		41		10.4
Grand total or average	All parents [c]	1,342		856		63.8		1,506		530		35.2	
	All hybrids		7,053		906		12.8		7,617		289		3.8

[a] With *Ustilago levis* (K. and S.) Magn.
[b] No smut was observed in any lines. Owing to unfavorable weather no infection occurred.
[c] No data are presented for Markton, as this variety produced no smut in either unhulled or hulled seed at any station in any year.

INFLUENCE OF HULLING ON INFECTION IN SELECTIONS FROM THE UNNAMED OAT C. I. NO. 357

Results were obtained also on relative smut infection occurring in selections of the unnamed oat C. I. No. 357, grown from unhulled and hulled seed. In all, 200 of these selections were grown in the experiment. Owing to lack of time, the seeds of only 100 selections were hulled for the 1925 crop. An equal number of seeds per row was sown in both the unhulled and hulled groups. Table 2 gives the total number of plants and the number of infected plants from unhulled and hulled seeds.

TABLE 2.—*Smut infection in plants grown from equal numbers of unhulled and hulled seeds of 200 selections made from the unnamed oat C. I. No. 357*

Condition of seed	Plants		
	Total	Infected	
	Number	*Number*	*Per cent*
Hulled	1,412	236	16.7
Unhulled	1,747	44	2.5

Hulling markedly reduced the number of plants that reached maturity, and increased the amount of infection. Only 2.5 per cent of the plants grown from unhulled seed were smutted, while 16.7 per cent of the plants grown from hulled seed were infected.

The influence of hulling the seed for the 1925 crop was evident in the 1926 progeny. Of 112 selections which showed no infection in 1925, 44 showed infection in the 1926 test when all seed was hulled. Of these 44 lines, 12 were grown from hulled seed and 32 from unhulled seed in 1925. Table 3 gives a summary of the 1926 data showing 1925 seed treatment.

TABLE 3.—*Smut infection*[a] *in the two plant groups resulting from 1925 seed treatment of 44 selections of the unnamed oat C. I. No. 357*

Selections (number)	Condition of seed	Plants grown at—					
		Aberdeen, Idaho			Moro, Oreg.		
		Total	Infected		Total	Infected	
		Number	*Number*	*Per cent*	*Number*	*Number*	*Per cent*
12	Hulled	441	14	3.2	313	3	1.0
32	Unhulled	1,042	80	7.7	780	43	5.5
Total or average		1,483	94	6.3	1,093	46	4.2

[a] With *Ustilago levis* (K. and S.) Magn.

The progenies of plants grown from seed that was not hulled the previous year showed more than three times as much infection in 1926 as the progenies originating from a hulled-seed source. This is conclusive evidence of the value of hulling for determining true smut susceptibility in oats.

Under the conditions of these experiments consistently higher infection was obtained by hulling the oat kernel. All of the parent

varieties other than Markton, with the possible exception of Scottish Chief, are moderately to highly susceptible to the smuts of oats. Even in these susceptible varieties, however, the glumes apparently offer considerable protection against infection.

The data for selections from the unnamed oat C. I. No. 357 emphasize the fact that susceptible strains can be eliminated more certainly if seed is hulled. Under field conditions a 100 per cent infection is rarely obtained even where hulling is practiced, but the number of escapes is fewer than when the hulls are not removed.

The data from these experiments are of interest in considering also the susceptibility of the naked oat (*Avena nuda*) to covered-smut infection. There is no reason to believe that *A. nuda* is inherently more susceptible than many varieties of *A. sativa*. Lacking the protection of hulls, it appears to be more highly susceptible. Resistance is the naked oat must be developed by crossing with varieties like Markton, which are truly resistant and are not smut-free merely because of hull protection.

INFLUENCE OF HULLING ON SEEDLING EMERGENCE

Limited data are available from the experiments conducted at Moro, Oreg., in 1926, on the influence of hulling on seedling emergence. The data are given in Table 4.

TABLE 4.—*Influence of hulling oat seeds on seedling emergence at Moro, Oreg., in 1926*

Variety	Seeds of each condition sown	Seedlings from uninoculated seed					
		Unhulled		Hulled		Reduction due to hulling	
	Number	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
Early Champion	760	592	77.9	511	67.2	81	10.7
Sixty-Day	760	572	75.3	540	71.1	32	4.2
Markton	680	532	78.2	503	74.0	29	4.3
Total or average	2,200	1,696	77.1	1,554	70.6	142	6.5

Variety	Seeds of each condition sown	Seedlings from seed inoculated with Ustilago levis					
		Unhulled		Hulled		Reduction due to hulling	
	Number	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
Early Champion	760	602	79.2	478	62.9	124	16.3
Sixty-Day	760	554	72.9	481	63.3	73	9.6
Markton	680	514	75.6	465	68.4	49	7.2
Total or average	2,200	1,670	75.9	1,424	64.7	246	11.2

Hulling reduced the number of seedlings emerging from uninoculated seed of all varieties 6.5 per cent and from seed inoculated with *Ustilago levis* 11.2 per cent. Smut inoculation influenced the emergence of seedlings, but hulling alone reduced the number of seedlings even slightly more than did the smut. The effect of hulling varied considerably with the variety. Early Champion, which produces a rather small caryopsis and is not especially vigorous, suffered an average reduction of 13.5 per cent, which was greater than that of any other variety. Hulling reduced by an average of 6.9 per cent

the emergence of seedlings in Sixty-Day, another variety with a small caryopsis but of greater vigor than Early Champion. Markton was affected less both by hulling and by inoculation than either of the other varieties. It seems rather significant, however, that even in Markton, which so far has shown no apparent evidence of smut infection, the seedling emergence was reduced by 2.9 per cent through inoculation with smut. If this may be accepted as evidence, it shows that Markton is not completely free from infection by the smut organism.

INFLUENCE OF HULLING ON NUMBER OF PLANTS REACHING MATURITY

In nearly all experiments in the present investigations in which hulled seed was compared with unhulled seed, a record was made of the number of seeds sown. As a result, some data were obtained on the influence of hulling on the number of plants that reached maturity. Where emergence counts are not available a comparison of the number of plants maturing from equal numbers of hulled and unhulled seed is of interest.

Data are available on this phase of the investigations from essentially the same varieties and hybrids used in the studies on the influence of hulling on smut infection. Likewise, data are available only for 1925 and 1926. These have been summarized and are shown in Table 5.

TABLE 5.—*Influence of hulling oat seeds on the number of plants reaching maturity*

Station and year	Generation of hybrid progeny	Variety crossed on Markton	Parents[a] or hybrids	Plants from—					
				Hulled seed			Unhulled seed		
				Seeds sown	Matured plants		Seeds sown	Matured plants	
				Number	*Number*	*Per ct.*	*Number*	*Number*	*Per ct.*
Aberdeen, Idaho:									
1925	F_3	Aurora, Idamine, Victory	Parents	750	511	68.1	750	621	82.8
			Hybrids	10,150	7,935	78.2	10,150	8,234	81.1
1926	F_4	Idamine, Victory	Parents	600	412	68.7	600	490	81.7
			Hybrids	2,700	1,910	70.7	2,700	2,150	79.6
Ames, Iowa, 1926	F_3	Idamine, Iogren, Silvermine, Victory	Parents	850	297	34.9	850	361	42.5
			Hybrids	8,200	2,962	36.1	8,200	3,547	43.3
Dickinson, N. Dak., 1925	F_3	Swedish Select	Parent	250	103	41.2	238	82	34.5
			Hybrid	6,200	2,722	43.9	5,989	3,008	50.2
Moro, Oreg., 1925	F_3	Scottish Chief	Parent	160	98	61.3	160	81	50.6
			Hybrid	3,280	1,183	36.1	3,280	1,778	54.2
Total or average			Parents	2,610	1,421	54.4	2,598	1,635	62.9
			Hybrids	30,530	16,712	54.7	30,319	18,717	61.7

[a] Data on Markton omitted from table.

In general, the data of Table 5 are consistent in indicating that hulling reduced the number of plants that reached maturity. Doubtless most of this reduction is traceable to failure of germination or emergence of seedlings.

At Aberdeen in 1925 the average percentage of plants maturing from hulled seed of the parent varieties and of hybrid selections was 68.1 and 78.2, respectively. For the unhulled seed the percentage was 82.8 and 81.1, respectively. More consistent results were ob-

tained at Aberdeen in 1926. In the two years at this station hulling reduced the number of plants reaching maturity on an average by 13.9 per cent in the parents and 4.2 per cent in the hybrid strains.

Results from Ames are available only for 1926. Owing in part to unfavorable weather conditions for germination and emergence, less than half the seed sown produced matured plants. However, the ratio in reduction caused by hulling is about the same in the parent varieties as in the hybrid strains, the average reduction being 7.6 and 7.2 per cent, respectively.

At Dickinson, N. Dak., and Moro, Oreg., also, a much smaller number of plants reached maturity from both hulled and unhulled seed. The data on Swedish Select and Scottish Chief, the parent varieties, show that more plants reached maturity from hulled than from unhulled seed. This is contrary to the results obtained from the hybrid strains at the same stations as well as to those from both parents and hybrids at all other stations. Soil inequalities and the small number of seeds sown probably account for this variation.

The data obtained at Dickinson on the hybrid selections are in conformity with those obtained at Ames and Aberdeen. Hulling the Markton × Swedish Select strains reduced the number of plants maturing by 6.3 per cent. In strains of the Markton × Scottish Chief cross at Moro, hulling reduced plant numbers by 18.1 per cent. This reduction is nearly three times that occurring at any other station. Unfavorable soil conditions at seeding time at Moro probably account for this wide departure.

The results indicate the value of the oat hull (lemma) as a protection to the caryopsis. They probably explain the low germination and rapid loss of germinating ability in the naked or hull-less oat.

In most cases a higher percentage of plants from hulled seed reached maturity from hybrid seed than from susceptible parent seed. The greater survival probably may be attributed to the greater vigor of the hybrids.

INFLUENCE OF HULLING ON CLASSIFICATION OF SEGREGATES IN STUDYING INHERITANCE OF SMUT SUSCEPTIBILITY AND RESISTANCE

Other writers have shown that hulling oats increases infection by smut. A comparison of the infection of hybrid segregates in populations grown from unhulled and hulled seed has not been reported heretofore. Some data of this nature are given in Table 6. The seeds from each F_2 plant were divided into two duplicate lots. The seeds of one lot were then hulled and those of the other were left unhulled. All seeds were inoculated. The seeds from each lot from each F_2 plant were sown in separate rows; that is, each row in each lot duplicated a comparable row in the other lot. The F_3 progenies were classified into four groups: (1) Those infected in the rows from only the hulled lot; (2) those infected in the rows from only the unhulled lot; (3) those infected in the comparable rows from both the hulled and unhulled lots; (4) and those not infected.

TABLE 6.—*Influence of hulling oat seeds on infection of F_3 hybrid progenies with Ustilago levis in 1925*

Variety crossed on Markton	Station	Number of progenies				
		Infected, from—			Not infected	Total
		Hulled seed only	Unhulled seed only	Seed in both lots		
Swedish Select	Dickinson, N. Dak.	42	4	28	50	124
Idamine	Aberdeen, Idaho	1	0	3	22	26
Victory	Aberdeen, Idaho	4	3	10	19	36
Aurora	Aberdeen, Idaho	19	6	42	74	141
Scottish Chief	Moro, Oreg.	30	4	14	47	95
Total		96	17	97	212	422

The proportions of infected populations from hulled and unhulled seed are very marked. Of the 422 F_3 progenies there were 96 infected only when the seed was hulled, 17 infected only when the seed was not hulled, 97 infected when the seeds were in comparable rows from both the hulled and unhulled lots, and 212 not infected at all. Assuming that the 96 lines infected only when the seed was hulled would have escaped infection in an experiment involving only unhulled seed, under such circumstances there would have been 308 smut-free and 114 infected progenies instead of the 212 smut-free and 210 infected actually obtained. The results would have compared favorably with those obtained by investigators from experiments in which hulling the seed before inoculation was not practiced.

Published observations record a decidedly larger percentage of smut-free progenies than of smut-infected progenies in crosses of resistant and susceptible varieties. The results here presented, derived through using hulled seed, indicate that previous data are not conclusive. Later tests in which hulled seed was used showed that additional strains apparently smut free in the F_3 generation were actually smut susceptible in later generations.

The increase in the number of infected strains apparently due to hulling the seed amounted to 22.8 per cent, a sufficient warrant for hulling the seed in conducting genetic studies on smut resistance under field conditions.

The data also emphasize the importance of developing inoculation methods for insuring complete infection. Until this is done it will not be possible to interpret satisfactorily studies on the inheritance of smut resistance or susceptibility.

SUMMARY

Removing the hull from the oat caryopsis before inoculation increased the percentage of smutted plants in susceptible varieties from 35.2 to 63.8 per cent.

In hybrid selections of these varieties with the smut-immune Markton oat, hulling increased the number of plants infected with *Ustilago levis* from 3.8 to 12.8 per cent.

In selections from the unnamed oat C. I. No. 357 hulling increased infection with *Ustilago levis* from 2.5 to 16.7 per cent. Of 112 lines showing no infection in 1925, 44 were infected with *U. levis* in a second

test when all seed was hulled. Of the 44 lines, 12 were grown from hulled seed and 32 were grown from unhulled seed in 1925.

In three varieties hulling reduced by 8.8 per cent the number of seedlings emerging from both inoculated and uninoculated seed. The influence of hulling on seedling emergence apparently varies with the variety.

The average percentage of plants reaching maturity in all tests was 54.7 for hulled and 61.8 for unhulled seed.

Hulling the seed in hybrid populations resulted in a marked increase in the number of smutted plants above that obtained when the seed was not hulled.

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